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STUDIES IN THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE) VII. THE GENUS *LEPIDAPLOA*

Harold Robinson

Abstract.—The Neotropical Vernonian genus *Lepidaploa* is recharacterized, nomenclaturally clarified, and its 116 species are listed. *Lepidaploa* has seriate-cymose inflorescences and lophate pollen surfaces of a type found in the related genera of the *Lepidaploa* Complex. *Lepidaploa* is distinct in the Complex by the sessile heads, the heads with 1.3–3.0 times as many involucral bracts as flowers, nodular style bases, sometimes glanduliferous achenes, and lack of glands on the anther appendages. Variations in exine patterns in *Lepidaploa* are compared with the three other genera of the Complex with rhizomatous crests, *Echinocoryne, Stenocephalum* and *Chrysolaena,* and the two genera with non-rhizomatous crests, *Lessingianthus* and *Mattfeldanthus.* New combinations are provided for 114 species, and two species, *L. beckii* and *L. solomonii* are described as new.

The present paper concludes a series of papers aimed at the resolution of the Neotropical *Lepidaploa* group in the tribe Vernonieae. Previous papers in the series have dealt with the five closely related genera of the informally defined *Lepidaploa* Complex, *Stenocephalum, Echinocoryne, Lessingianthus, Chrysolaena* and *Aynia* (Robinson 1987a, b, 1988a, b, c) that differ from *Vernonia* s. str. by having consistently lophate pollen, and with two less closely related genera, *Cyrtocymura* and *Eirmocephala* (Robinson 1987c), that usually have true scorpioid cymes. The remaining genus *Lepidaploa* of the *Lepidaploa* Complex having lophate pollen is treated in the present paper.

Lepidaploa was named originally by Cassini (1817b) as a subgenus of *Vernonia* with brief comments on distinctions from the other two subgenera accepted at that time. Six species were mentioned in association with the subgenus, *Vernonia glauca, V. fasciculata, V. arborescens, V. divaricata, V. scorpioides* and *V. albicaulis,* in that order.

The genus was treated more fully five years after the original description (Cassini 1823), but was still referred to as a subgenus. Generic status of *Lepidaploa* is sometimes erroneously dated from the 1823 treatment (Gleason 1906:174) because of the combinations under *Lepidaploa* included in that treatment. *Lepidaploa* was not given generic status until it was listed in a series of genera by Cassini (1825) in his treatment of the genus *Oliganthes.* The latter listing mentioned no included species.

The proper characterization of *Lepidaploa* dates from the treatment of the subgenus by Cassini in 1823. The subgenus was given the alternative French name *Lépidaple,* and was described as having involucral bracts "régulierement imbriquées, appliquées, subcoriaces, lancéolées, acuminées et presque spinescentes au sommet; les intérieures étrécies de bas en haut, terminées en pointe, nullement élargies, arrondies, ni colorées au sommet." Cassini (1823) clearly distinguished his subgenus from typical *Vernonia* by the lack of a subulate appendage and lack of coloration on the bracts of the involucre. The lack of bract

appendages also distinguished *Lepidaploa* from the paleotropical subgenus *Ascaricida* (=*Baccharoides* Moench) based on *Vernonia anthelmintica* L. (Cassini 1817a, b). In 1823 Cassini included seven species in the subgenus *Lepidaploa, L. scorpioides* (from *Vernonia scorpioides*), *L. phyllostachya* (same as the earlier *V. arborescens*), *L. aristata, L. albicaulis* (from *V. albicaulis*), *L. lanceolata* (=?*V. longifolia*), *L. canescens* (from *V. canescens*) and *L. buxifolia* in that order. The most notable difference between the 1823 and 1817 listings was the elimination of the two species of *Vernonia* from eastern North America, *V. glauca* and *V. fasciculata.* The latter belong to the *Vernonia* s. str. close to the type, *V. noveboracensis.* Cassini further cited additional species of *Vernonia* mentioned by Kunth (Humboldt et al. 1818) that were "presque indubitables" members of the subgenus *Lepidaploa, V. gracilis, V. tournefortioides* (=*V. scorpioides*), *V. geminata, V. mollis, V. pellita, V. micrantha* and *V. frangulaefolia.* None of the Cassini names or combinations in *Lepidaploa* were valid as of the 1823 publication since *Lepidaploa* was not at that time recognized at the generic level.

A precise typification of the subgenus *Lepidaploa* was not attempted until almost 100 years after the original description. Gleason (1906:165) rather incidentally stated that *Lepidaploa* was based on *V. scorpioides.* To the extent that this can be regarded as a serious lectotypification, this appears to have been an arbitrary selection of the first species listed by Cassini in 1823. The incidental and arbitrary nature of the selection allows the rejection of the unrepresentative species as lectotype. Robinson et al. (1980:428), in a review of subdivisions of the Vernonieae, listed *Lepidaploa* with the lectotype *Vernonia albicaulis,* which is far more representative of the species given by Cassini in 1823. The value of the latter lectotypification has been confirmed in the present series of studies, since *Lepidaploa* can now represent a broader group following its traditionally broader interpretation by such authors as Baker (1873). *Vernonia scorpioides,* which has traditionally represented a narrower concept as a section or series *Scorpioideae,* has now been treated as the type species of a smaller well-defined segregate genus *Cytocymura* (Robinson 1987c).

Shortly after the lectotypification by Robinson et al. (1980), Jones (1980) listed *Lepidaploa* in the synonymy of *Vernonia* with *Vernonia glauca* (L.) Willd. cited as the type. At present, no earlier history for this typification is known. The choice was evidently again an arbitrary selection of the first species listed by Cassini in 1817(b). Such an arbitrary lectotypification would not have to be rejected, but *V. glauca* is an undesirable selection for *Lepidaploa* in view of Cassini's subsequent failure to include the species in the subgenus (1823). The choice is further undesirable because *V. glauca* is an immediate relative of the type species of *Vernonia, V. noveboracensis,* and it usually has shortly appendaged involucral bracts of the type that Cassini (1823) pointedly indicated were lacking in his subgenus *Lepidaploa.* One must conclude that Cassini's (1817b) original inclusion of *V. glauca* in *Lepidaploa* was based on an inadequate understanding of that species. The specimen no. 8428 on the Jussieu herbarium (sheet no. 8428, IDC microedition 6206, fiche 620) that was seen by Cassini seems to have essentially no appendages on the involucral bracts.

The lectotypifications by Gleason (1906) and Jones (1980) share one particularly unwholesome aspect associated with their arbitrary nature. Both attempts were treating *Lepidaploa* only as a synonym of *Vernonia* with no concern for its possible importance as a taxon in its own right. The arbitrary nature of the selections allows for rejection, and the poor choices involved make rejection desirable, even if both had priority.

A major part of the confusion regarding the concept of *Lepidaploa* arises from Cassini's reliance upon the involucral bracts as

a character. Some typical *Vernoniae* such as *V. fasciculata* lack appendages on the bracts, while many species now recognized as *Lepidaploa* possess narrowly pointed involucral bracts. Appropriately, Cassini seemed to place little confidence in his 1817 subgenus. The changed listing of species by Cassini in 1823 created a more closely related group with only one species, of those identifiable with modern concepts, lacking seriate-cymes and only two of those species proving, on later examination, to have non-lophate pollen. Unfortunately, Cassini did not accompany his improved grouping with an improved description. Nevertheless, Cassini's confidence in the group had risen sufficiently by 1825 to recognize *Lepidaploa* at the generic level. During the period from 1825 to 1841 a number of authors recognized *Lepidaploa* at the generic level: Cassini (1825), Reichenbach (1828), Bartling (1830), Cassini (1830), and Spach (1841).

DeCandolle (1836) and later major authors did not treat *Lepidaploa* at the generic level. DeCandolle (1836) retained *Lepidaploa* as his section VIII of *Vernonia* containing 195 species including some from Asia and Africa. The type species of *Vernonia* was placed in the section IX. *Ascaricida* (including *Bacchariodes*).

Bentham (Bentham & Hooker 1873) broadened the concept of *Lepidaploa* within *Vernonia* to include a series *Paniculatae* which included the type species of *Vernonia,* but he restricted the subgenus *Lepidaploa* geographically to, "Species Americanae ultra 200." The *Lepidaploa* concept of Bentham and his followers such as Baker (1873), Gleason (1922), and Jones (1979b) came to include all American *Vernonia* with unappendaged involucral bracts and a double pappus. As such, the concept included the type of *Vernonia* and fell into the synonymy of the subgenus and section *Vernonia.*

The resurrection of *Lepidaploa* in the present paper is nearly in the sense of Cassini in 1823, though it traces nomenclaturally to the confused concept of 1817. As defined herein, the genus *Lepidaploa* includes 116 species distributed throughout the Neotropical Region, many species occurring in the West Indies, the Andes, and Brazil, and a smaller number occurring in Central America. The genus includes most of the Neotropical species formerly placed in *Vernonia* that have heads in well-developed seriate-cymes as described below. The genus does not include some species with markedly scorpioid seriate-cymes such as *Cyrtocymura scorpioides* and *Eirmocephala brachiata* (Robinson 1987c) or many seriate-cymose members of *Lessingianthus* (Robinson 1988a) and *Mattfeldanthus* (Robinson & King 1979). The distinguishing features such as the sessile heads, reduction in size of inflorescence bracts, styles with well-developed basal nodes, fusion of veins in the corolla lobes, glands on the achenes, lack of glands on the anther appendages, and details of the rhizomatous crests on the pollen are discussed more fully under separate headings.

Inflorescence Form

The inflorescences of the Asteraceae are generally cymose; the great majority of the species, and most Vernonieae, including those in typical *Vernonia,* have a distinctly cymose structure. The inflorescence forms in the tribe have been discussed by many authors (Gleason 1923, Cabrera 1944, Jones 1979b). Some of the inflorescence branches become aligned in a series and may achieve a scorpioid form. The branches are usually marked by heads borne singly or in groups at a series of nodes. In the extreme, each branch appears superficially spicate or racemose in a form that has been referred to by most as a scorpioid cyme. In this series of studies the use of the latter term is restricted to inflorescences such as those of *Cyrtocymura* and *Eirmocephala* which are actually scorpioid, and the more common non-scorpioid forms in the Vernonieae are

referred to with the more broadly applicable term seriate-cyme (Figs. 61, 62; Robinson 1987c, 1988a). The extreme forms of seriate-cymose inflorescences in the Vernonieae with heads appearing lateral and sessile are nearly restricted to the few related groups of almost exclusively Neotropical distribution that are treated in the present series of papers on the *Lepidaploa* Complex.

In these inflorescences each branch appears spicate but is actually a series of lateral proliferations. As noted by Gleason (1923) and Cabrera (1944), each head is developmentally terminal and only appears lateral as a result of its displacement by a lateral branch produced at its base. The resulting structure in the Neotropical members of the tribe varies in appearance from a spike to an obvious scorpioid cyme. The most obviously scorpioid forms occur in the more remotely related Neotropical genera with type A pollen, *Cyrtocymura, Eirmocephala* (Robinson 1987c), and *Dipterocypsela,* and in one African species *Vernonia peculiaris* Verdcourt, but the seriate cymes with heads appearing lateral and sessile are otherwise almost completely restricted to the immediate *Lepidaploa* Complex of genera having lophate pollen.

Within the Complex, the seriate-cymes with apparently sessile heads occur in *Lepidaploa* itself, as well as in *Chrysolaena* Robinson (1988b), some of *Lessingianthus* Robinson (1988a), *Mattfeldanthus* Robinson & King (1979), and *Stenocephalum* Sch.Bip. (Robinson 1988a). Variations of the inflorescence with the heads raised on short or long peduncles occur in *Aynia* Robinson (1988c), *Echinocoryne* Robinson (1987b), and many other species of *Lessingianthus.* One of the most distinctive features of *Lepidaploa* appears to be the consistency of the sessile heads. The only distinctly pedunculate heads in the genus are those that are terminal on the branches and a few rare non-terminal pedunculate heads in such species as *V. cleocalderonae* and *V. macahensis,* and specimens such as Wilbur 13260 from Panama illustrated by Keeley (1982). The terminal peduncles really differ from the other heads only in the lack of a subsequent lateral branch, but the presence of a peduncle on a lower head, which is exceedingly rare in *Lepidaploa,* can be interpreted developmentally as a downward displacement of the succeeding lateral branch. The presence of apparent peduncles is comparatively common throughout most of the diversity of the related genus *Lessingianthus.* Thus, while seriate-cymes occur in both *Lepidaploa* and *Lessingianthus,* the "pedunculate" forms are essentially restricted to the latter genus in the pair. The "non-pedunculate" seriate-cyme that is characteristic of *Lepidaploa* and *Mattfeldanthus* is closer to the condition in the sessile-headed but less seriate inflorescences in many other Vernonieae, and it occurs to some extent in all but one genus of the *Lepidaploa* Complex where it appears to be primitive. The "peduncles" in *Lessingianthus* and *Echinocoryne* are rather individually distinctive in the tribe and are considered as derived separately in each of those genera.

As noted by various authors (Baker 1873, Gleason 1923), there is variation in the degree of development of the bracts that are located at the series of nodes in the seriate-cyme. The genera *Cyrtocymura, Dipterocypsela,* and *Eirmocephala* have minute bracts that are scarcely visible under the heads. Members of the more restricted *Lepidaploa* Complex usually have more obvious foliose bracts subtending the heads at each node of the series, but the bracts may vary in size from slightly larger than minute to essentially the size of the vegetative leaves. The bracts of *Mattfeldanthus* and *Stenocephalum* are essentially like vegetative leaves. The bracts of *Chrysolaena* are very small. The bracts in *Lepidaploa* and *Lessingianthus* show contrasting trends in their relative size. Species of *Lessingianthus* with sessile heads subtended by foliose bracts in a seriate-cyme have the bracts similar in

size to the vegetative leaves that are below the inflorescence. There is little or no abrupt change in size of foliose elements at the base of the inflorescence. In *Lepidaploa,* the bracts at the base of the inflorescence are almost always at least slightly discontinuous in size from the vegetative leaves immediately below them (Figs. 61, 62), and the inflorescence often has very reduced bracts. In only a few species of *Lepidaploa,* such as the Brazilian *V. obtusifolia,* is there no evident reduction in the size of the foliar structures starting at the base of the inflorescence.

Involucral Bracts

The involucre of *Lepidaploa* is significant for both the ratio of bracts to flowers in the heads and for the differentiation of the bracts.

There has been no systematic study of the ratio of involucral bracts to flowers in the heads of the Vernonieae. Nevertheless, significant differences in the ratios have become evident from counts made during the description of various species and genera. Differences in the ratio are sometimes simply a reflection of the overall number of flowers. In *Stenocephalum* (Robinson 1987a), the higher percentage of bracts is primarily related to the reduced number of flowers, whereas in *Lepidonia* (Robinson & Funk 1987), the nearly equal number of bracts and flowers is related to the comparatively large number of flowers in the heads. In the case of *Echinocoryne* and the type species of *Mattfeldanthus,* the ratio is altered by the extremely high number of involucral bracts in the heads. In *Chrysolaena* the imbalance of the ratio derives from the unusually small number of bracts in the head. Nevertheless, there are also differences in the ratio in some groups that lack extremes in numbers of bracts or flowers. In the type species of *Vernonia* and its immediate relatives, the number of bracts and flowers seems nearly equal, but in *Lepidaploa* and *Lessingianthus* the bracts are usually one and a half to three times as numerous as the flowers.

Many species of *Lepidaploa* have strong differentiation between the outer and inner involucral bracts. The outer bracts are more pointed and are often aristate. The inner bracts are usually blunt with at most a short mucro. A common pattern in the genus is a lower cluster of spreading, slender bracts contrasted with the more erect and appressed, less pointed, inner bracts. Such a pattern occurs in a few species of *Lessingianthus* such as *L. niederleinii,* but the larger heads usually distinguish the members of the latter genus with such involucres from *Lepidaploa.*

Veins of Corolla Lobes

During various studies of the family I have noted that the veins in the corolla lobes of the Vernonieae are more completely fused at the tip than those of many other tribes of the Asteraceae, and in the present study most members of the *Lepidaploa* Complex have been seen to have veins that fuse at the apex more broadly than those in most other species of the Vernonieae. In *Aynia* and *Mattfeldanthus* the fusion is extreme and the lobe tip is filled with a large sclerified shield (Robinson 1988c). Species of *Chrysolaena* have the narrowest veins distally and the weakest fusion of any members of the Complex. *Lepidaploa* and *Lessingianthus* both show a moderate thickening of lobe veins and a further moderate enlargement in the apical fusion that falls far short of the extreme form. Still, the latter is greater than that in most genera of the Vernonieae outside of the Complex such as *Vernonia* s str.

Basal Stylar Node

In *Lepidaploa* the style base characteristically has a large zone of spreading, thick-walled cells that result in a very large disc in dried plants. It is this structure that is

here referred to as a basal stylar node. The sclerified disc is sharply angled inward under the base of the style and it leaves a comparatively narrow central area of attachment. Styles of *Lessinginathus, Stenocephalum, Echinocoryne,* and *Chrysolaena* show little or no zone of thick-walled cells at the base and they have no large basal disc. The disc is not sharply angled under the base of the style and the area of attachment is not or scarcely narrower than the style shaft.

There is no functional basis known for the differences in style bases of the members of the *Lepidaploa* Complex, and the changes in style base form must be considered rather rare and essentially random. Nevertheless, style base differences correlate closely with the generic limits in the *Lepidaploa* Complex. This pattern shows the comparative continuity within each genus compared to the broad phyletic gaps between the genera.

Glands on Achenes and Anther Appendages

Short-stalked, capitate glands that produce sesquiterpene lactones are common in the Vernonieae as glandular punctations on the surface of various structures in different genera. *Lepidaploa* often has glands on the achene surface, while *Lessingianthus* never has such glands. In most *Lepidaploa,* the glands occur among the long setulae that cover the achenes, but a few species such as *V. macahensis* from the Rio de Janeiro region, have glanduliferous achenes without setulae.

Glands occur on the anther appendages of various Vernonieae, including three elements among the genera treated in the present series of studies: one of the three species of *Eirmocephala, E. cainarachiensis* (Hieron.) H. Robinson (Robinson 1987c), one specimen of *Lepidaploa* that was identified as possibly *V. helophila,* and six of the seven species of the genus *Chrysolaena.* The remaining related genera, *Aynia, Echinocoryne, Lepidaploa, Lessingianthus, Mattfeldanthus,* and *Stenocephalum,* seem to lack glands except in the one case mentioned above. The various species mentioned in which the glands occur on the appendages, including the species of *Eirmocephala,* are all in groups that also have glands on the achenes.

Pollen

The *Lepidaploa* Complex is characterized by pollen with crests in a lophate pattern, and it includes most of the Neotropical species with lophate pollen that are traditionally placed in the genus *Vernonia* (Figs. 1–54). A lophate pattern occurs also in the phyletically distinct Old World element of the Vernonieae (Figs. 55–58) and ultimately in the related tribe Lactuceae. It has been concluded in this series of studies that the complex and widely occurring lophate form is more primitive than the non-lophate, spinose grains called the *Lychnophora* type by Stix (1960) and Type A by Jones (1979b). Cases of reversion to Type A pollen from lophate forms have been cited in the Old World *Distephanus* Cassini (Robinson & Kahn 1986) and in the Neotropical *Lessingianthus* (Robinson 1988a); other such reversions I presume have occurred many times. Accordingly, the pollen of the *Lepidaploa* Complex is considered to have retained the more primitive pattern in the tribe.

Within the *Lepidaploa* Complex there are further distinctive details of the pollen that can be used in the classification. The variation in structure of the basal columellae under the crests partially correlates with generic concepts, but a SEM is necessary to observe the character. In *Lepidaploa* the columellae show a type that is referred to here as rhizomate or rhizomiform (Figs. 1–51), where the columellar material is weakly attached to the foot layer and is often nearly completely diverted at the base into a horizontal structure (Figs. 6, 15, 16, 25, 30, 33). The rhizomatous crests of this *Lepidaploa*

type are known only from the Neotropical *Lepidaploa* Complex in the genera *Lepidaploa, Chrysolaena, Echinocoryne,* and *Stenocephalum* (Robinson 1987a, b, 1988b) and from one species of *Eirmocephala* (Robinson 1987c). The contrasting form, with separate columellae strongly attached to the foot-layer (Figs. 52–56), occurs in diverse elements of the tribe including the Neotropical *Lessingianthus* (Figs. 52, 53), *Aynia,* and *Mattfeldanthus* (Fig. 54) of the *Lepidaploa* Complex, and the African genera such as *Baccharoides* Moench. (Figs. 55, 56). Horizontal structures under the crests in paleotropical Vernonieae such as *Cyanthillium* Blume (Figs. 57, 58) are totally different, being bridges between strongly attached points at the intersections of the crests. Because of the comparatively restricted nature of the rhizomate form, it is regarded as a derived condition in this study.

Within the restricted *Lepidaploa* Complex, a few complications in the pattern of the basal columellar structure are seen, but these are more apparent than real. Firstly, one species of *Mattfeldanthus* has distinct horizontal structures under its pollen crests, but these are intermittent bridges like those of *Cyanthillium.* Secondly, some species of *Lepidaploa* have the rhizomes absent or poorly developed, but these differ from the typical *Lessingianthus* type by the tendency for the columellae under the crests to be narrow and less strongly attached to the foot-layer (Figs. 3, 8, 12, 18, 31, 37–39, 42, 51). The less rhizomate forms in *Lepidaploa* are commonest within the genus in species with Type D pollen.

A taxonomically useful characteristic of the pollen that can be seen with a light microscope is the pattern of the areoles on the surface of the grain. The pollen types that are of significance in the *Lepidaploa* Complex are considered in the following order: Type B, Type C, *Aynia* Type, Type G, and Type D. Of the pollen Types, only B and D seem to characterize related groups, and none characterize a whole genus.

Type B pollen.—The pollen areolation that has been called the *Vernonia argyrophylla*-type by Stix (1960) and Type B by Jones (1979b) is distinguished by colpi that extend from pole to pole with no separate polar areoles and by three equatorial areoles across the intercolpar area in a 1:2:1:2:1 or rarely 1:2:3:2:1 pattern. Type B pollen occurs primarily in *Lessingianthus* subg. *Lessingianthus* (Fig. 52), but grains in some species of *Lepidaploa* also have a third equatorial role in some of their intercolpar regions (Figs. 23, 26, 45, 50). None of the latter has the third areole characteristically in all the intercolpi, and none has strong basal columellae like those of *Lessingianthus.* The intercolpar region in *Lepidaploa* usually differs by having a 1:2:2:1 pattern (Figs. 5, 11, 14, 29, 36, 46) in the C, D, G, and *Aynia* Types.

Type C pollen.—Many species of *Lepidaploa,* including the type species, show pollen grains that have a polar areole. The areole is positioned at the apices of the three colpi. Such grains were called the *Vernonia cognata*-type by Stix (1960) and Type C by Jones (1979b). Type C pollen with rhizomatous crests occurs in *Chrysolaena* (Robinson 1988b) and *Stenocephalum* (Robinson 1987a) of the *Lepidaploa* Complex, and a Type C pollen with non-rhizomatous crests is found in the small subgenus *Oligocephalus* of *Lessingianthus* (Robinson 1988a).

There is a significant variation within the Type C pollens that occur in *Lepidaploa.* The Andean and West Indian elements of the genus are sometimes erratic in the expression of the polar areole. One pole may have the areole while the other end does not. This is often a consistent feature of grains in a species, and the difference probably reflects the relative outward or inward facing positions of the poles in the original pollen tetrads. It would seem a slight loss for neither pole to have an areole, and the Central American *V. tortuosa,* with technically Type G pollen, might have Type C ancestry. Some of the species showing variable poles also have the crests particularly

thick on each side of the pores (Figs. 2, 4, 10), a condition reminiscent of Type A grains. The species of *Lepidaploa* with Type C grains that are found in Brazil have characteristically narrower crests (Fig. 17), and they consistently have areoles at both poles.

A number of species with Type C pollen, *Vernonia cleocalderonae* (Figs. 17, 18) from central Brazil, and *V. cotoneaster* (Figs. 12, 18) of a group found in eastern Brazil and northern South America, have basal columellae that are partially non-rhizomatous. Such columellae have been noted elsewhere in *Lepidaploa* only in the members with Type D pollen areolation that is discussed below. In contrast, the West Indian *V. sericea* (Fig. 6), the widely distributed *V. salzmannii* (Figs. 15, 16), and to a lesser extent, *V. canescens* (Fig. 8) of the northern Andes have crests with rhizomiform baculae that peel away from the footlayer comparatively easily.

Aynia Type pollen.—*Vernonia tovarensis* (Figs. 19–24) seems to have a pollen form that is unique in *Lepidaploa* in having the intercolpar areoles nearest the poles actually reaching the poles (Fig. 19). The colpi terminate about half way between the pores and the poles. The pattern of areoles is known from only the one species in *Lepidaploa,* but is the same areolation found in *Aynia* and the comparatively unrelated Central American genus *Harleya* Blake. As in *Aynia,* the crosswalls above and below the pores show a sutural line in the middle, but none of the grains of either *Aynia* or *V. tovarensis* show separation at the median suture of the crosswalls, and it is not possible to say at this time whether they only meet or actually fuse. In spite of the similar areolation, the exine differs from that of *Aynia* by the modification of the basal columellae into a rhizomiform structure of the type found in most of *Lepidaploa.*

Type G pollen.—The majority of species of *Lepidaploa,* especially in Brazil, have Type G pollen that does not have areoles centered at the poles of the grains and does not have crosswalls in the colpi (Figs. 25–33). In these characters the pollen is like Type B of Jones (1979b) or *Vernonia argyrophylla*-type of Stix (1960), and no distinction was made in those earlier studies. More recently the Jones and Stix terms have been applied more narrowly to pollen of the type found in *Lessingianthus* (Robinson 1988a), with three equatorial areoles across the intercolpi and nonrhizomatous columellae. The Type G pollen in *Lepidaploa* usually has intercolpar areoles in a 1:2:2:1 pattern correlated with obviously rhizomiform baculae as seen under the SEM (Figs. 27, 30, 31, 33). The seemingly slight difference has proven one of the more phyletically significant ones in the *Lepidaploa* Complex. The closest approach to the Type B pollen areolation in a species of *Lepidaploa* is in *V. psilostachya* DC. where the colpi reach the poles and there is a variable number of 2 or 3 areoles across the intercolpus in 1 or 2 tiers (Figs. 25–27). Examination shows that even in this species very few of the grains have 3 areoles across all the intercolpi simultaneously. A third intercolpar areole is even less common in other species with Type G pollen.

Type G pollen was earlier distinguished by the author as the *Vernonia geminata*-type (Robinson 1980). Unfortunately, the use of the name *geminata*-type now appears inappropriate as a result of the present study. The Colombian name *Vernonia geminata* H.B.K. was misapplied to a Brazilian species with Type G pollen. The Colombian species is a synonym of *V. canescens* having Type C pollen. The Brazilian species with Type G pollen should have been identified as *V. subsquarrosa.* The present paper adopts the term Type G for pollen that has been previously called the *geminata*-type. The letter is the next that would follow in the series used by Jones for his two studies (1979b, 1981).

Type G pollen is closest to Type C pollen in its structure, and the species involved seem to be interrelated. Type G pollen seems

to occur in Brazilian species that are reasonably close in relationship to some others of that area with Type C pollen. Some species of the Andes of Peru and Bolivia such as *V. retrosetosa* and *V. tristis* seem to be possible relatives of Brazilian species. However, the Type G pollen in the central American *V. tortuosa* and the Colombian *V. sclareaefolia* and *V. trilectorum* seems separately derived from more closely related Andean members of *Lepidaploa* having Type C pollen. A brief survey of some andean species shows those with Type G pollen lack resiniferous idioblasts on the achene surface, whereas those with Type C pollen often have such idioblasts.

Type G grains are found outside of *Lepidaploa* in the related genus *Echinocoryne,* and non-rhizomatous grains with similar areolation are seen in the less closely related *Mattfeldanthus.*

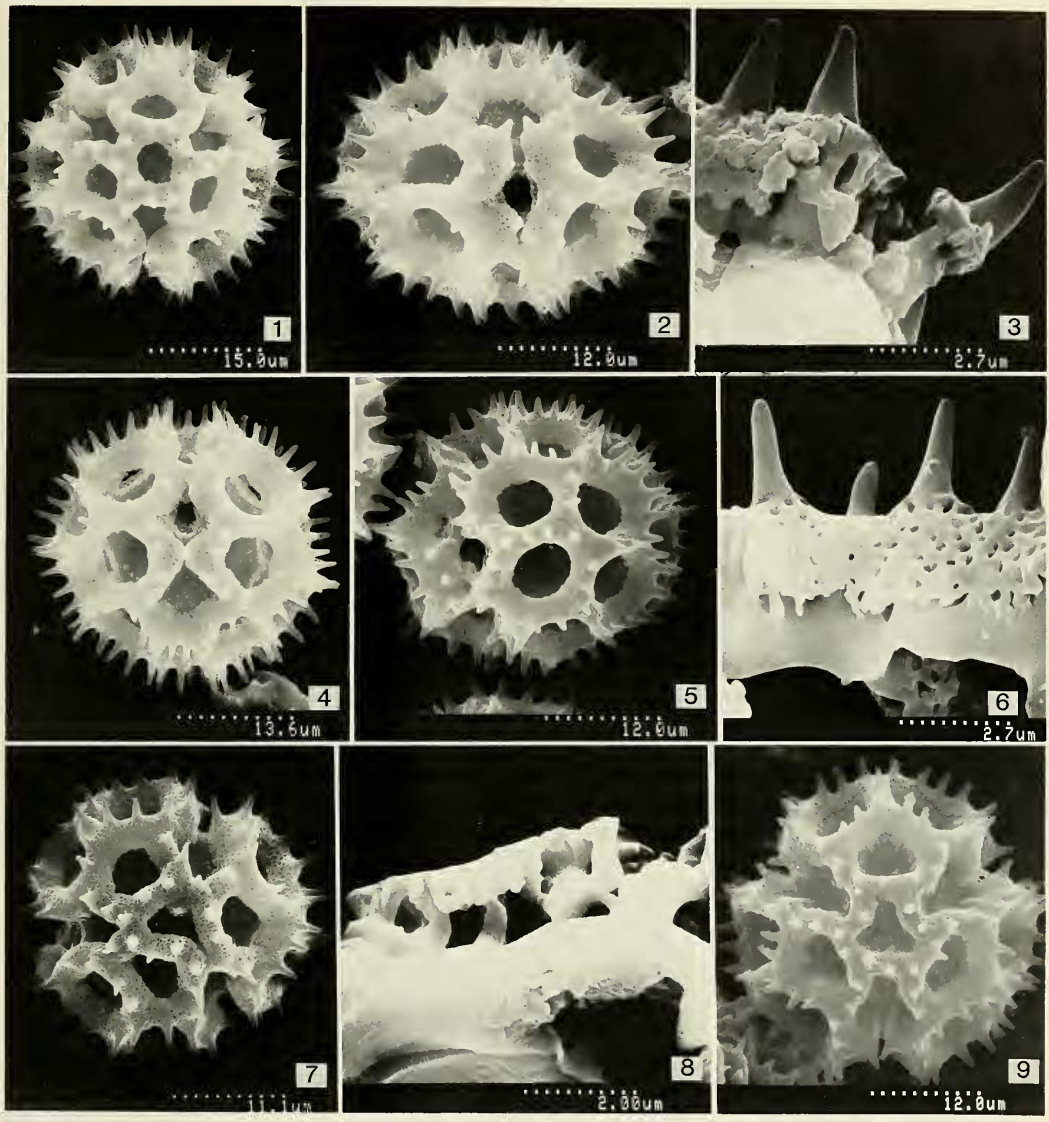
Type D pollen.—A final pollen type within *Lepidaploa* is that referred to by Stix (1960) as the *Vernonia arenaria*-type and by Jones (1979b) as Type D (Figs. 34–51). The intercolpus has a 1:2:2:1 or sometimes a 1:2:1:2:1 areolation pattern and there are no areoles centered on the poles, but the colpus is not continuous. The grains are distinctive by the presence of crosswalls above and below the pore which divide each colpus into three sections (Figs. 35, 40, 41, 44, 49). These are not the partial intrusions into the colpus that are seen in some grains of other pollen types; rather, these crosswalls are complete, unbroken crests. Type D pollen is almost restricted to *Lepidaploa,* but grains with similar crosswalls occur in two species of *Lessingianthus.* Pollen of the two *Lessingianthus* species (Robinson 1988a) differs from that of *Lepidaploa* by the consistency of the 1:2:1:2:1 intercolpar pattern and the strong unconstricted basal columellae. The weak columellae of the Type D pollen in *Lepidaploa* are stronger than those of most members of their genus, but they are not mistakeable for the type found in *Lessingianthus.* The two species of *Lessingianthus* have long-pedunculate heads and they are not particularly like *Lepidaploa* in any feature except the pollen.

The group of species in *Lepidaploa* with Type D pollen is one of the most natural subdivisions in the genus. The distinctive areolation and the trend toward stronger basal columellae in the pollen is correlated in many of the species with a distinctive pubescence of T-shaped hairs on their stems and leaves. The appearance of the pubescence varies from densely sericeous to totally appressed, and it is not matched in other members of *Lepidaploa.*

The essentially non-rhizomatous columellae of the Type D pollen in *Lepidaploa* is interpreted here as a reversion from the rhizomatous condition. There is an irregularity and partial fusion in those columellae and constriction of the bases (Figs. 37–39, 42, 47, 51) not seen in *Lessingianthus.* Only a few other species, such as *V. cotoneaster* and *V. cleocalderonae,* with Type C pollen, have been noted as having similar basal columellae (Figs. 12, 18). In all of these, the columellae show at least some tendency toward the rhizomatous condition, and in a few parts of some grains rhizomiform columellae are present (Figs. 37–39, 42).

Limitations and exclusions.—Although some pollen types evidently reflect related groups within the genus *Lepidaploa,* a subdivision of the genus by pollen alone would be artificial. Only the species with Type D pollen are considered to constitute a phyletic group among themselves. Species with the Type G pollen appear to relate to at least two different elements of the species group having pollen Type C, but these pollen types reflect large groups of species, and they predominate in different geographical areas. Taxonomic subdivisions in the latter group are not expected to coincide completely with the limits of the pollen types. No special status is foreseen for the one Venezuelan species with *Aynia* Type pollen.

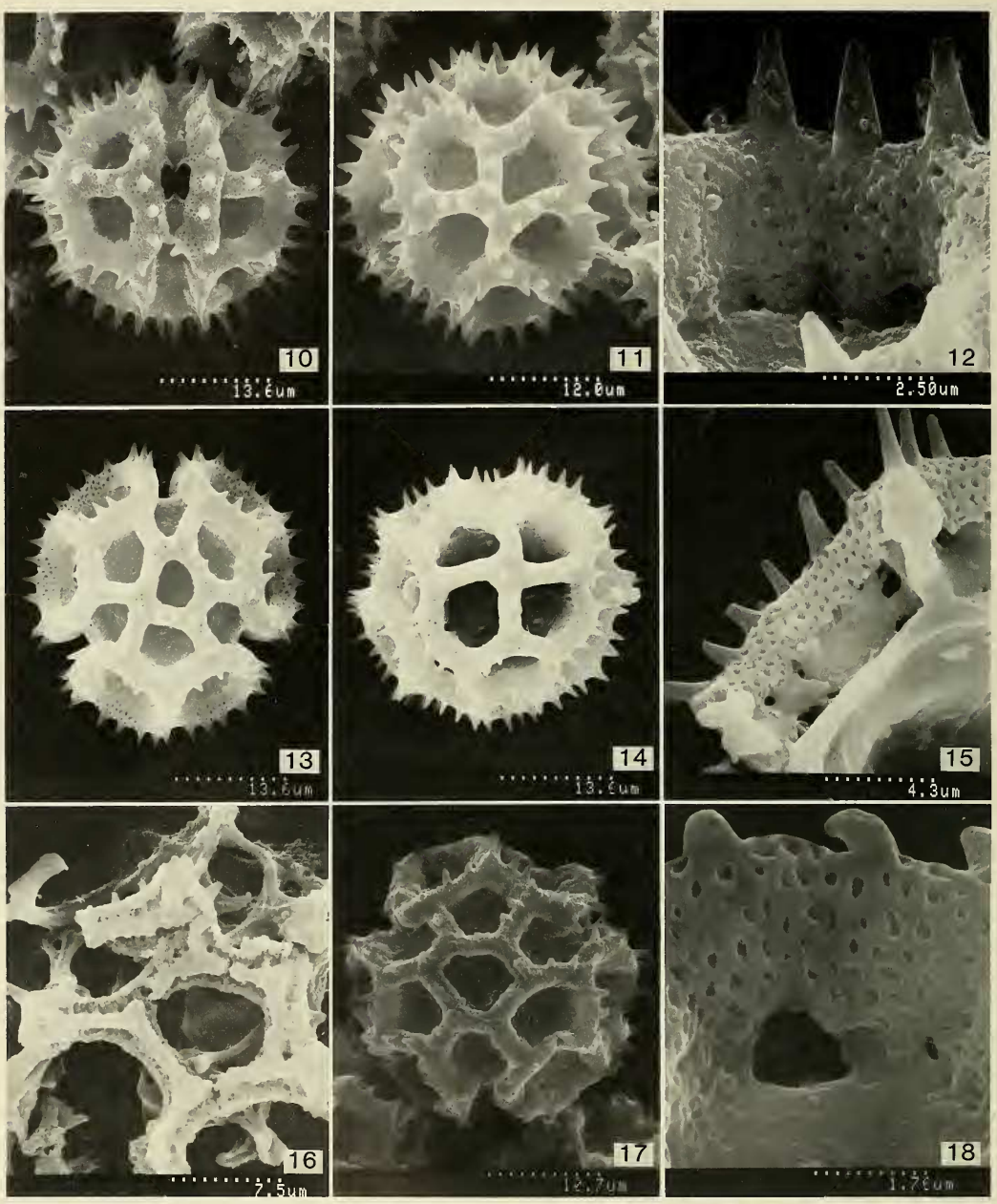
In the following undivided alphabetical list of the species of *Lepidaploa,* the pollen



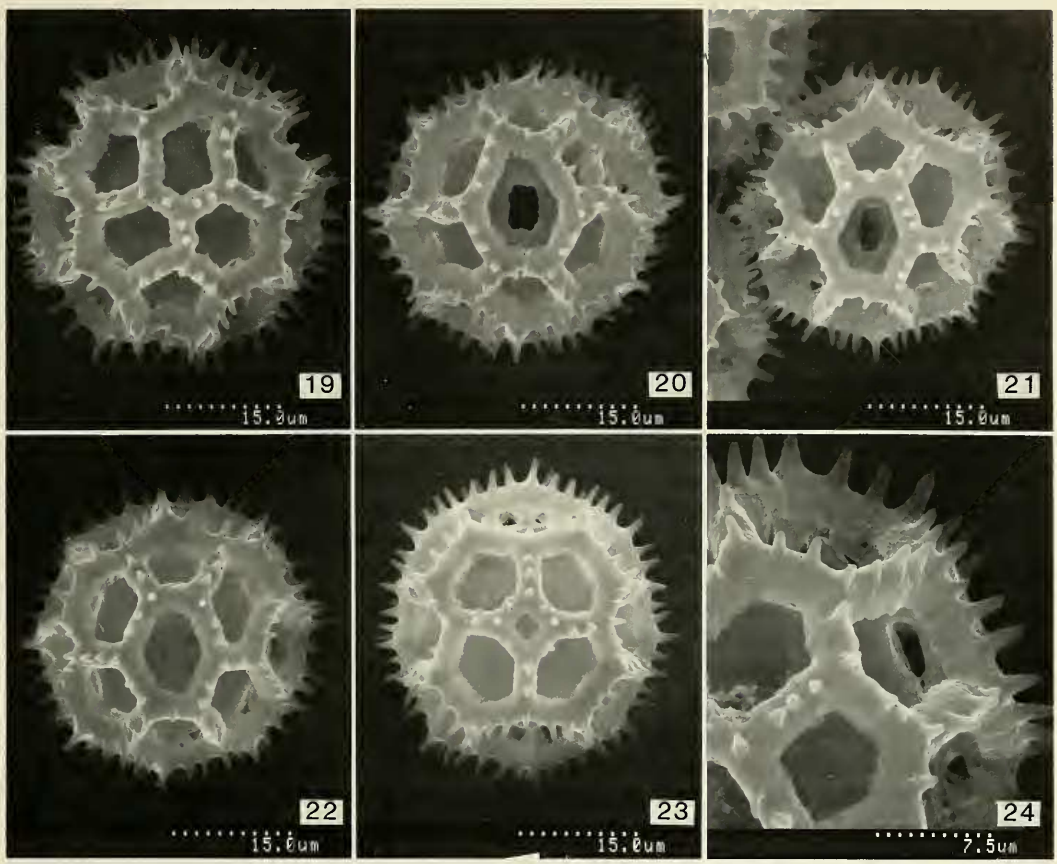
Figs. 1–9. *Lepidaploa,* Type C pollen. 1–3. *L. arborescens* from St. Vincent, Morton 5721. 1. Polar view. 2. Colpar view. 3. Broken grain showing baculae. 4–6. *L. sericea* from Haiti, Leonard 8990. 4. Colpar view. 5. View showing intercolpus. 6. Crest of grain showing rhizomiform baculae broken away from footlayer. 7, 8. *L. canescens* from Ecuador, Hitchcock 20342. 7. Polar view. 8. Broken grain showing baculae. 9. *L. cotoneaster* from Brazil, King & Bishop 8620, polar view.

types are indicated under each of the species as C, D, G, *Aynia* Type, B/G for G Types with a tendency for Type B areolation, and C/G for pollen with polar areoles usually at only one pole.

One Neotropical species examined in this study, *Acilepidopsis echitifolia* (Mart. ex DC.) H. Robinson (1989), synonym *Vernonis ararana* Gardn., of Brazil and Paraguay, has lophate pollen and shows some features that suggest relationship to *Lepidaploa.* However, examination of the pollen (Figs. 59,



Figs. 10–18. *Lepidaploa,* Type C pollen. 10–12. *L. cotoneaster* from Brazil, King & Bishop 8620. 10. Colpar view. 11. Intercolpar view. 12. Detail of crest showing baculae. 13–16. *L. salzmannii* from Peru, Ferreyra 9327 (13, 14); from Brazil, Hatschbach 43889 (15, 16). 13. Polar view. 14. Intercolpar view. 15. Broken grain showing rhizomiform baculae weakly attached to footlayer. 16. Detached exine showing rhizomiform baculae from below. 17, 18. *L. cleocalderonae* from Brazil, Calderon et al. 2689, holotype. 17. Polar view. 18. Detail of crest showing baculae.



Figs. 19–24. *Lepidaploa tovarensis* pollen, from Venezuela, Pittier 12794, isotype. 19. Polar view showing three intercolpar areoles meeting at pole. 20–22. Colpar views showing crosswalls with distinct median sutures. 23. Intercolpar view. 24. Detail of crests showing modified baculae.

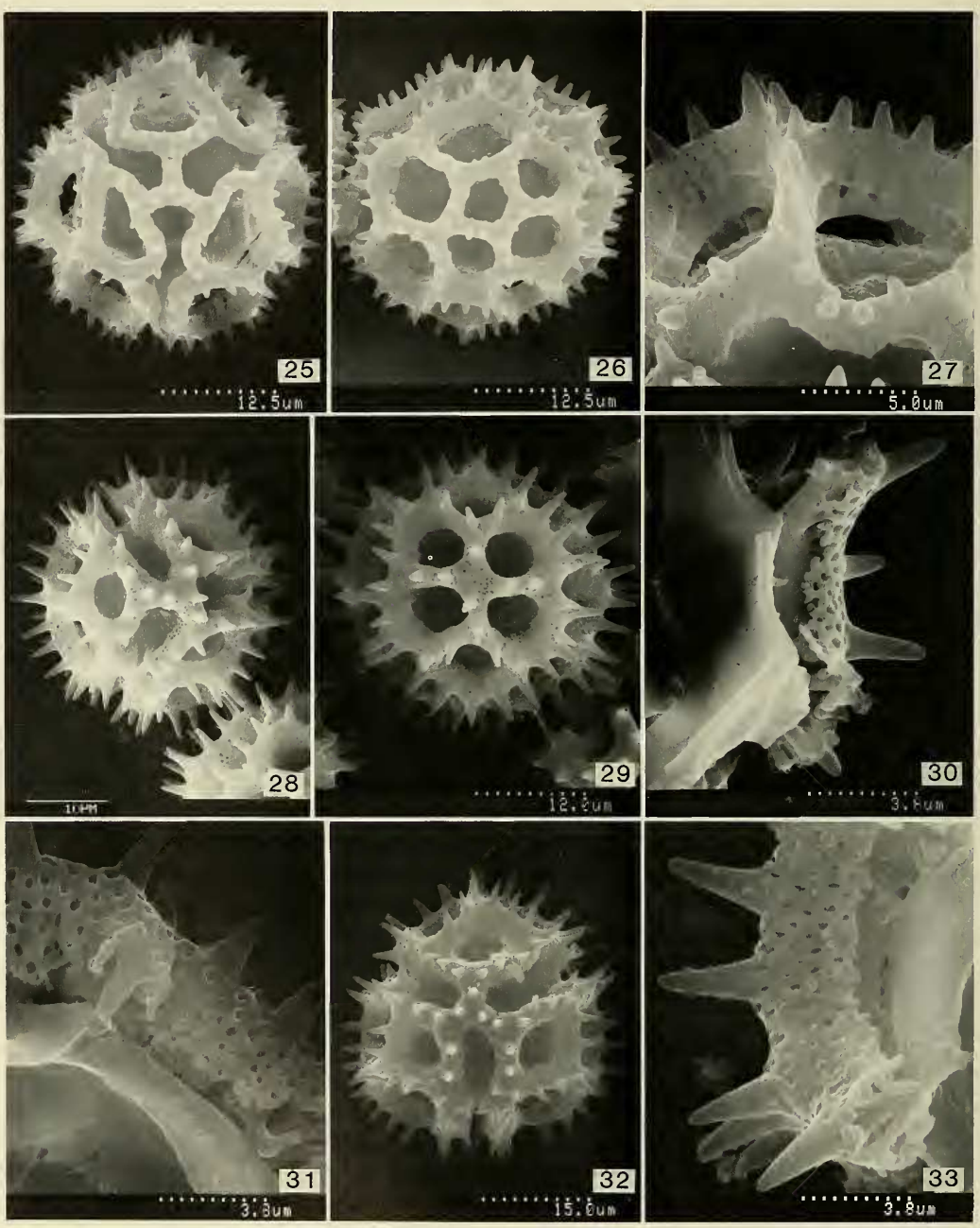
60) shows a type that is called Type E by Jones (1981) in his survey of the Old World members of the tribe. Such pollen is not otherwise known from any *Vernonia sensu lato* native to the Neotropical region. The form of the pollen strongly suggests that the species is actually most closely related to Old World members of the tribe such as the African *Vernonia polysphaera* Baker and the Asian *Acilepis squarrosa* D. Don that have the same type of pollen (Kingham 1976; Jeffrey 1988). Large reddish glands, branched inflorescences, and procumbent bases of the stems help to distinguish the South American *Acilepidopsis* from possible relatives in both hemispheres (Robinson 1989).

Geography

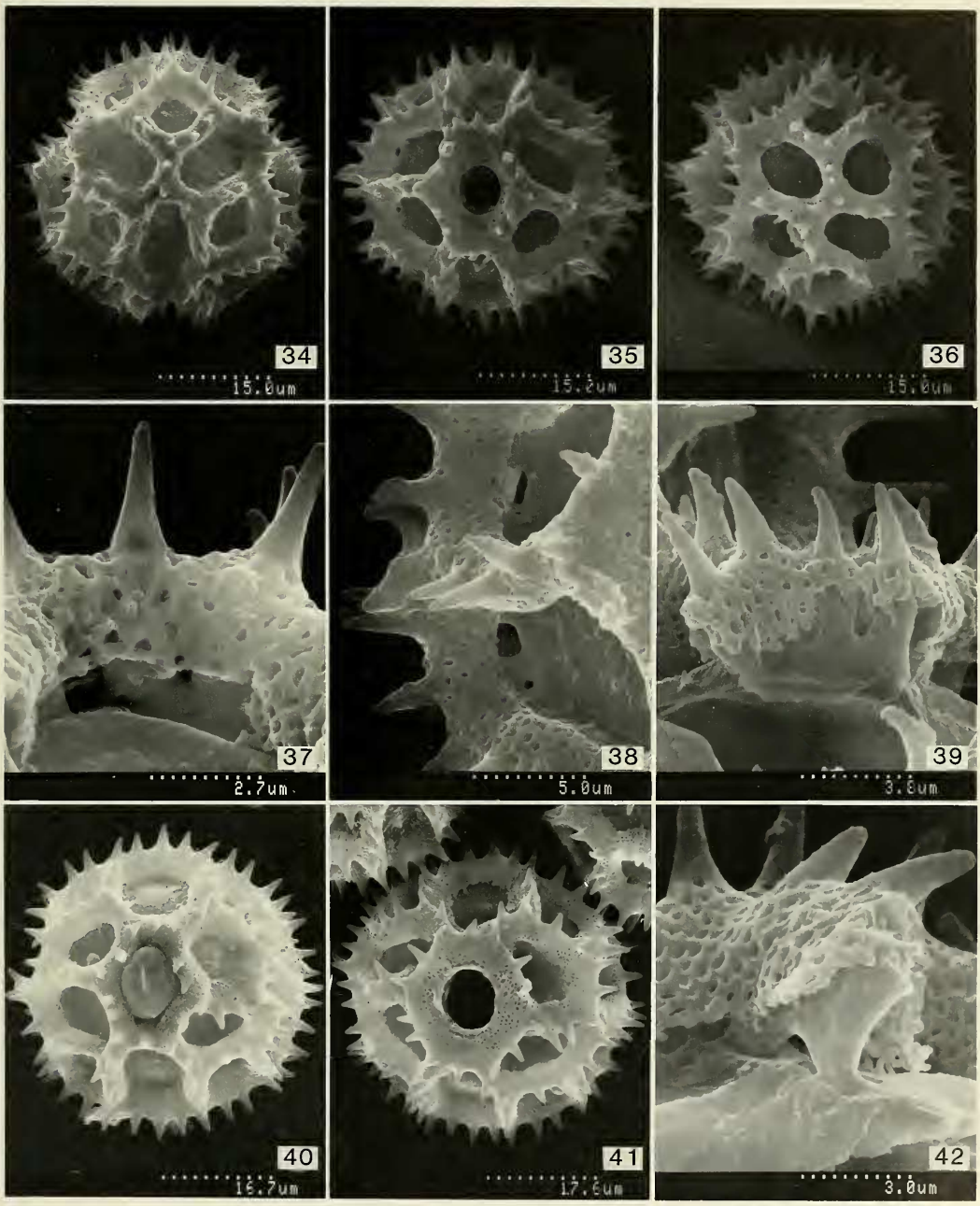
Lepidaploa has the most extensive geographical range of any genus in the related Complex, occurring from Mexico and the West Indies southward through most of montane or savanna areas of South America. In contrast, the other genera are all predominantly or exclusively Brazilian, except the monotypic *Aynia* of Peru.

Chromosome Number

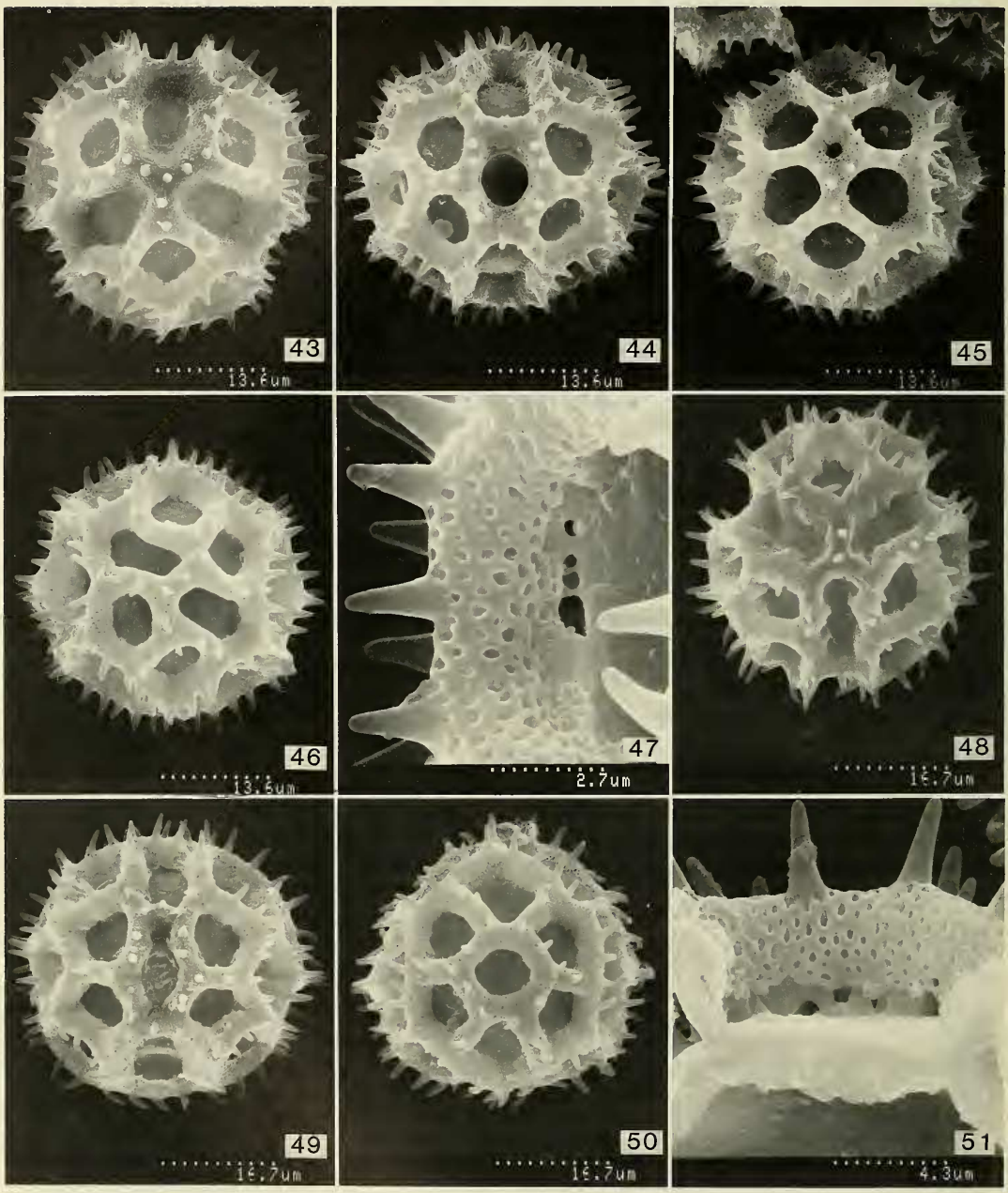
All available counts (Jones 1979a, Keeley 1978) indicate that the *Lepidaploa* Complex has the New World pattern of $n = 17$ chromosomes (Jones 1977). Eleven species of *Lepidaploa* have been counted, including



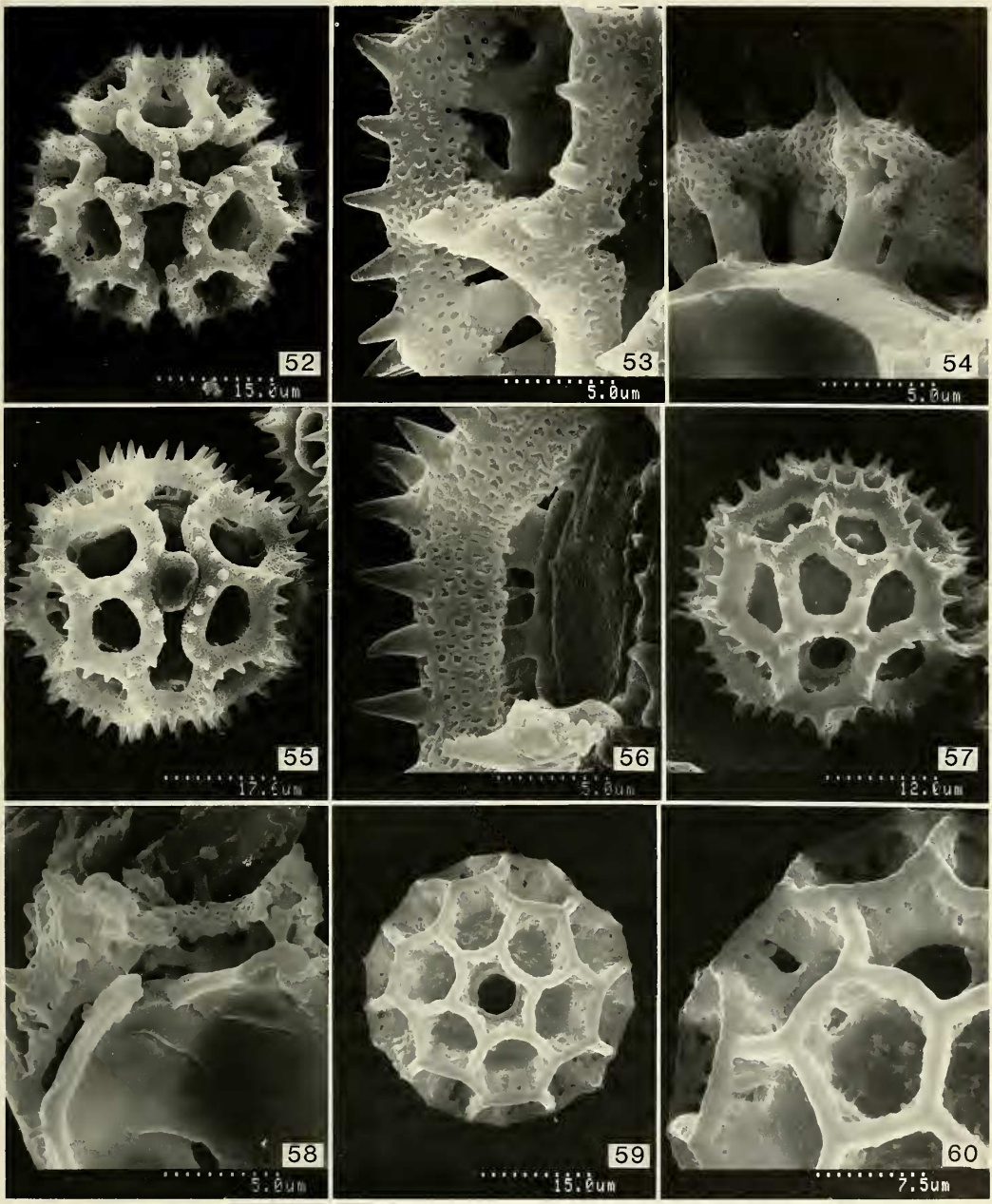
Figs. 25–33. *Lepidaploa,* Type G pollen. 25–27. *L. psilostachya* from Brazil, Riedel & Lund 1745/590. 25. Polar view. 26. Intercolpar view. 27. Detail of crests showing rhizomiform baculae. 28–31. *L. subsquarrosa* from Brazil, Rose 20194 (28–30) and Mimura 491 (31). 28. Polar view. 29. Intercolpar view. 30, 31. Broken grains showing rhizomiform baculae. 32, 33. *L. persericea* from Brazil, Mori et al. 13700. 32. Polar view. 33. Broken grain showing rhizomiform baculae weakly attached to footlayer.



Figs. 34–42. *Lepidaploa,* Type D pollen. 34–39. *L. aurea* from Brazil, Irwin et al. 14595. 34. Polar view. 35. Colpar view showing crosswalls. 36. Intercolpar view. 37–39. Details of crests showing modified baculae. 40–42. *L. tombadorensis* from Brazil, Harley et al. 22906. 40, 41. Colpar views showing crosswalls. 42. Broken grain showing crest with modified baculae.



Figs. 43–51. *Lepidaploa,* Type D pollen. 43–47. *L. chalybaea* from Brazil, Mori & Benton 13094. 43. Polar view. 44. Colpar view showing crosswalls. 45, 46. Intercolpar views showing variation in areole pattern. 47. Detail of crest showing modified baculae and weak attachment to footlayer. 48–51. *L. rufogrisea* from Brazil, Cuatrecasas & Duarte 26641. 48. Polar view. 49. Colpar view showing crosswalls. 50. Intercolpar view. 51. Detail of crest showing modified baculae.



Figs. 52–60. Various lophate pollen types in the Vernonieae. 52, 53. *Lessingianthus rubricaulis* from Colombia, Pennell 10657. 52. Polar view. 53. Detail of crests showing baculae. 54. *Mattfeldanthus nobilis* from Brazil, Hatschbach 50443, broken grain showing baculae. 55, 56. *Baccharoides adoensis* from Rhodesia, Best 336. 55. Colpar view. 56. Detail of crest showing baculae. 57, 58. *Cyanthillium patula* from the Philippines, Steiner 468. 57. View showing pore. 58. Broken grain showing partial rhizomiform bridges under crests. 59, 60. *Acilepidopsis echitifolia* from Paraguay, Pedersen 3269. 59. View showing pore. 60. Detail of crests showing baculae.

one hexaploid, *V. trinitatis*. The base number has also been reported for other genera of the Complex, *Lessingianthus* (Robinson 1988a) and *Chrysolaena* (Robinson 1988b), but the latter genera both show an incidence of tetraploidy that has not yet been reported from *Lepidaploa*.

The known chromosome numbers are given with the pollen type under the species in the taxonomic summary.

Further Distinctions

A number of Brazilian species such as *Vernonia subsquarrosa* have insect galls of a type mentioned in the original description of *V. alvimii* (Robinson 1980). The galls are actually achenes infested with Dipteran larvae so that they grow larger than normal. They are fat and rather fusiform with a much reduced pappus. Such achenes have not been seen in the related genera such as *Lessingianthus*.

None of the species of *Lepidaploa* have the generally larger size of all floral parts that is common in *Lessingianthus*. Only one species belonging to *Lepidaploa, Vernonia eriolepis,* was placed in the *Vernonia* section *Lepidaploa Macrocephalae* of Baker (1873) that included many species now placed in *Lessingianthus*. *Lepidaploa eriolepis* has some of the smallest floral parts of any species that was included in that section. The difference in size of floral parts in the genera seems to extend to the width of the style shaft and to some extent to size of the pollen. The somewhat larger pollen of *Lessingianthus* may be a factor in the common occurrence of extra intercolpar areoles in that genus.

The difference in average size of floral parts in *Lepidaploa* and *Lessingianthus* is like that which sometimes results from higher chromosome numbers. However, the basic numbers of the two genera both seem to be $n = 17$. Some of the specimens of *Lepidaploa* with larger pollen, approaching that of *Lessingianthus* in size, may have higher ploidy levels as in *V. trinitensis,* but the larger size in *Lessingianthus* seems to be achieved without increase in chromosome number. Future studies should attempt to measure actual DNA content.

Taxonomic Summary

The genus *Lepidaploa* is delimited in the present series of studies in the following manner.

Lepidaploa (Cassini) Cassini

Lepidaploa (Cassini) Cassini *in* G. Cuvier, Dict. Sci. Nat. 36:20. 1825; 60:586. 1830. Rchb., H. G. L., Consp. Regn. Veg. I:99. 1829 [1828]; Bartl., F. G., Ord. Nat. Pl. 136. 1830; Spach, E., Hist. Nat. Vég. 10: 39. 1841.

Vernonia subg. *Lepidaploa* Cassini, Bull. Sci. Soc. Philom. 1817:66. 1817.

Vernonia sect. *Lepidaploa* (Cassini) DC., Prodr. 5:26. 1836.

Annual or perennial herbs or shrubs, erect to spreading, to 1.5(–3.0) m tall; stems, leaves, and involucral bracts sparsely scabrid to sericeous or weakly tomentose, often glandular-punctate. Leaves alternate (opposite in *L. canescens* var. *opposita*), sessile to shortly petiolate. Inflorescence cymose with short or long seriately cymose branches, subcapitular bracts slightly to markedly smaller than nearest vegetative leaves. Heads sessile, broadly campanulate; bracts of involucre 1.3–3.0 times as numerous as florets in the head, unappendaged, in 3–6 series, outer bracts often slender and more spreading with aristate tips, inner bracts persistent, usually more erect and acute. Flowers (8–)10–35 in a head; corollas usually lavender, narrowly funnel-form, throats short but distinct, lobes bearing long hairs, spicules, glands, or with combinations, veins broadly fused at tips of lobes; anther appendages non-glanduliferous (except possibly in *L. helophila*); style base with an expanded node and with sclerified cells be-

low. Achenes prismatic, mostly 8–10-ribbed, usually densely long-setuliferous, often with glands on the surface, with or without resiniferous cells; carpopodia stopper-shaped or turbinate, extending upward among the bases of the lowest setulae, the cells oblong with porose lateral walls; inner pappus of numerous long capillary bristles, about as long as the corolla, outer pappus of distinct shorter scales. Pollen grains 45–50(–60) μm in diameter, lophate with crests rhizomatous or incompletely columellate, columellae narrower at base when present, crest pattern usually with two equatorial intercolpar areoles, sometimes with polar areoles (type C), with crosswalls above and below pores (type D), or with colpi continuous to the poles (type G).

Lectotype: *Vernonia albicaulis* Vahl ex Pers. [=*Lepidaploa glabra* (Willd.) H. Robinson].

The genus *Lepidaploa* can be credited with the following 116 species. The synonymy given below includes basionyms of the accepted species, basonyms of species placed in synonymy, and any subsequent combinations of these names at the species level in *Vernonia*. Synonymies generally follow Keeley (1978) for the West Indies, Aristeguieta (1964) for Venezuela, Jones (1980) for Peru, Cabrera (1944) for Argentina, and have been influenced by Baker (1873) in some of the older names from Brazil.

Lepidaploa acutiangula (Gardn.) H. Robinson, comb. nov.

Vernonia acutiangula Gardner, London J. Bot. 5:225. 1846. Brazil (Maranhão). Pollen C.

Lepidaploa acuminata (Less.) H. Robinson comb. nov.

Vernonia acuminata Less., Linnaea 6:663. 1831. *V. expansa* Gleason, Bull. New York Bot. Gard. 4:186. 1906. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa alvimii (H. Robinson) H. Robinson, comb. nov.

Vernonia alvimii H. Robinson, Phytologia 45:168. 1980. Brazil (Bahia). Pollen G.

Lepidaploa araguensis (Badillo) H. Robinson, comb. nov.

Vernonia araguensis Badillo, Bol. Soc. Venez. Ci. Nat. 10:283. 1946. Venezuela. Pollen C.

Lepidaploa araripensis (Gardn.) H. Robinson, comb. nov.

Vernonia araripensis Gardner, London J. Bot. 5:222. 1846. Brazil (Pará). Pollen C.

Lepidaploa arborescens (L.) H. Robinson, comb. nov.

Conyza arborescens L., Syst. Nat. ed. 10, 2: 1213. 1759. *Vernonia arborescens* (L.) Swartz, Fl. Ind. Occid. 3:1320. 1806. *V. divaricata* Swartz, Fl. Ind. Occid. 3:1319. 1806. *V. divaricata* Less., Linnaea 4:306. 1829. *V. icosantha* DC., Prodr. 5:49. 1836. *V. albicoma* Gleason, Bull. New York Bot. Gard. 4:185. 1906. *V. intonsa* Gleason, Bull. New York Bot. Gard. 4:182. 1906. *V. permollis* Gleason, Bull. New York Bot. Gard. 4:179. 1906. *V. ventosa* Gleason, Bull. New York Bot. Gard. 4:179. 1906. *V. amarantina* Gleason, Bull. Torrey Bot. Club 40:307. 1913. *V. parvuliceps* Ekman, Ark. Bot. 13(15):71. 1914. Antilles, Pollen C, Figs. 1–3; N = 17 (Keeley 1978).

The present concept differs from that of Keeley (1982) by its restriction to Antillean material. Separate specific status is restored for the continental material that was placed in synonymy by Keeley. The continental species is discussed under the name *Lepidaploa canescens*.

Lepidaploa arbuscula (Less.) H. Robinson, comb. nov.

Vernonia arbuscula Less., Linnaea 6:664. 1831. *V. arcuata* Gleason, Bull. Torrey

Bot. Club 33:185. 1906. *V. obcordata* Gleason, Bull. Torrey Bot. Club 33:187. 1906. *V. bahamensis* Griseb., Fl. Brit. W. Ind. 352. 1861. Bahamas. Pollen C; N = 17 (Keeley 1978).

Lepidaploa arenaria (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia arenaria Mart. ex DC., Prodr. 5: 54. 1836. *V. sarmentiana* Gardner, London J. Bot. 5:221. 1846. Brazil (Bahia, Piauhy). Pollen D.

Lepidaploa argyrotricha (Sch.Bip. ex Baker) H. Robinson, comb. nov.

Vernonia argyrotricha Sch.Bip. ex Baker in Mart., Fl Bras. 6(2):96. 1873. Brazil (Goiás, Espirito Santo, Minas Gerais, Rio de Janeiro). Pollen C; N = 17 (Keeley 1978).

Lepidaploa aristosquamosa (Britton) H. Robinson, comb. nov.

Vernonia aristosquamosa Britton, Bull. Torrey Bot. Club 18:332. 1891. Bolivia. Pollen G.

Lepidaploa aronifolia (Gleason) H. Robinson, comb. nov.

Vernonia aronifolia Gleason, Bull. Torrey Bot. Club 40:323. 1919. Cuba. Pollen C/G.

Lepidaploa aurea (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia aurea Mart. ex DC., Prodr. 5:58. 1836. Brazil (Bahia, D.F., Goiás, Minas Gerais). Pollen D, Figs. 34–39.

Lepidaploa auyantepuiensis (Aristeg.) H. Robinson, comb. nov.

Vernonia auyantepuiensis Aristeg., Acta Bot. Venez. 2(5–8):362. 1967. Venezuela. Pollen C.

The species seems close to *Lepidaploa ehretiifolia* Benth. but the pubescence of the stems and leaf undersurfaces is coarser and more erect. Also, the pollen is larger (nearly 60 μm in diam.), and there are usually three intercolpar areoles as in Type B pollen. The size of the grains and the coarseness of the hairs may indicate the species is a polyploid.

Lepidaploa barbata (Less.) H. Robinson, comb. nov.

Vernonia barbata Less., Linnaea 4:287. 1829. Brazil (Bahia, Mato Grosso, Minas Gerais). Pollen D.

Lepidaploa bakerana (Britton) H. Robinson, comb. nov.

Vernonia bakerana Britton, Bull. Torrey Bot. Club 18:331. 1891. Bolivia. Pollen C.

Lepidaploa beckii H. Robinson, sp. nov.

Plantae suffrutescentes et interdum subvolubiles 1.4–3.0 m longae laxe ramosae. Caulis brunnei et atrescentes dense sordide velutini. Folia alterna, petiolis 5–10 mm longis dense velutinis; laminae ovato-lanceolatae 15–27 cm longae et 6–11 cm latae base rotundatae ad quintum basilares latissimae margine integrae vel minime remote crenulatae apice breviter anguste acuminatae supra virides in nervis insculptae tenuiter sericeae subtus pallidiores in nervis valde exsculptae perdense sericeae vel sublanatae, nervis secundariis utrinque 14–18. Inflorescentiae dense ramosae in ramis primariis distincte bractiiferae, bracteis foliiformibus plerumque 3–9 cm longis et 1–3 cm latis, bracteis ramulis subnullis. Capitula sessilia in nodis binata vel congesta breviter campanulata 5–6 mm alta; squamae involucri plerumque virides interiores distaliter brunnescentes ca. 40 subimbricatae 3–4-seriatae lanceolatae 1.5–4.0 mm longae et 0.5–1.0 mm latae plerumque extus dense pilosulae et apice subaristatae, interiores sparse minute puberulae apice breviter acutae saepe recurvatae. Flores ca. 30 in

capitulo. Corollae albae 4.0–4.5 mm longae extus inferne glabrae distaliter et in marginis lobarum dense spiculiferae, tubis infundibularibus ca. 2 mm longis, faucibus ca. 1 mm longis, lobis oblongo-lanceolatis ca. 2 mm longis et 0.6 mm latis; thecae antherarum ca. 2 mm longae, appendicibus apicalibus ca. 0.5 mm longis glabris; basi stylorum abrupte disciformes. Achaenia ca. 2 mm longae dense sericeo-setuliferae non glandulferae distincte mediocriter idioblastiferae; setae pappi flavae ca. 40 plerumque 3.5–4.0 mm longae superne sensim distincte latiores in sereibus anguste lanceolatae ad 0.8 mm longae. Grana pollinis in diametro ca. 45 μm valde lophata, reticula in typo C. (Fig. 61).

Type.—Bolivia: La Paz: Prov. Nor Yungas, Suapi 16 km hacia Santa Rosa, 1650 m, bosque montañoso, sub-arbusto de 2 m erecto, frutos, en el borde del camino, 25.9.1987, St. G. Beck 13640 (holotype US; isotype LPB).

Paratypes.—Bolivia: La Paz: Prov. Murillo, Suapi 22 km hacia Santa Rosa de Quilo Quilo, 1300 m, restos del monte en el borde del camino, arbusta trepanda alga voluble, frutos en globulos, 25.9.1987, St. G. Beck 13638 (LPB, US); Valley of the Rio Zongo, approx. ½ hour by trail which climbs from the Cahua Hydroelectric Plant on the left bank of the Río Zongo, moist forest with scattered chacos, 16°05′S, 68°03′W, scandent shrub, stems up to 3 m, 23 Apr 1982, J. C. Solomon 7563 (MO; US); Prov. Nor Yungas, 5.5 km below Coroico towards Yolosa (1.4 km above Yolosa), disturbed roadside forest, 1400 m, 16°13′S, 67°44′W, suffrutescent, 1.5 m, corollas white, 16 May 1985, J. C. Solomon 13726 (MO, US), 21.1 km al noroeste del camino entre Yolosa y Caranavi por el camino a Suapi (ca. 2.5 km al oeste de Suapi, cerca del puente sobre el Río Suapi), bosque húmido muy tocado, 16°07′S, 67°47′W, 1200 m, corolas blancas, tallos arqueados hasta 3 m, 27 May 1988, Solomon 18400 (MO, US).

The species is readily distinguished by the large, coarse leaves having rounded, nearly sessile bases and veins impressed in the upper surface. The inflorescence is also distinctive in the branches with many small crowded heads that mostly lack obvious subcapitular bracts. The corollas seem to be unique in having the margins of the lobes densely spiculiferous along their whole length.

Lepidaploa bolivarensis (Badillo) H. Robinson, comb. nov.

Vernonia bolivarensis Badillo, Bol. Soc. Venez, Ci. Nat. 23(103):291. 1963. *Vernonia glandulosa* Badillo, Bol. Soc. Venez. Ci. Nat. 10:283. 1946, not *V. glandulosa* DC., Prodr. 5:22. 1836. Guyana, Venezuela. Pollen C.

Lepidaploa borinquensis (Urban) H. Robinson, comb. nov.

Vernonia borinquensis Urban, Symb. Antill. 3:390. 1903. Puerto Rico. Pollen C/G.

Lepidaploa buchtienii (Gleason) H. Robinson, comb. nov.

Vernonia buchtienii Gleason, Amer. J. Bot. 10:302. 1923. Bolivia. Pollen G.

Lepidaploa canescens (H.B.K.) H. Robinson, comb. nov.

Vernonia canescens H.B.K., Nov. Gen. Sp., folio ed. 4:27. 1818. *V. mollis* H.B.K., Nov. Gen. Sp., folio ed. 4:28. 1818. *V. geminata* H.B.K., Nov. Gen. Sp., folio ed. 4:28. 1818. *V. bullata* Benth. ex Oerst., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1852:67. 1853. *V. arborescens* var. *cuneifolia* Britton, Bull. Torrey Bot. Club 18:311. 1891. *V. sodiroi* Hieron. ex Sodiro, Bot. Jahrb. Syst. 29:1. 1900. *V. volubilis* Hieron., Bot. Jahrb. Syst. 36:460. 1905. *V. hirsutivena* Gleason, Bull. New York Bot. Gard. 4:175. 1906. *V. patuliflora* Rusby, Bull. New York Bot. Gard. 4:376. 1906. *V. purpusii* T. S. Brandegee, Univ. Calif. Publ. Bot.

Fig. 61. Holotype of *Lepidaploa beckii* H. Robinson, Beck 13640 (US).

6:197. 1915. *V. cuneifolia* (Britton) Gleason, Amer. J. Bot. 10:301. 1923, not *V. cuneifolia* Gardner, London J. Bot. 5:215. 1846. *V. pseudomollis* Gleason, Amer. J. Bot. 10:307. 1923. *V. rusbyi* Gleason, Amer. J. Bot. 19:753. 1932, based on *V. arborescens* var. *cuneifolia* Britton. *V. polypleura* Blake, J. Wash. Acad. Sci. 28: 478. 1938. *V. medialis* Standl. & Steyerm., Publ. Field. Mus. Nat. Hist., Bot. Ser. 23:148. 1943. *V. spiritu-sancti* Cuatr., Bot. Jahrb. Syst. 77:58. 1956. *V. unillensis* Cuatr., Bot. Jahrb. Syst. 77:59. 1956. Mexico, Guatemala, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia. Pollen C, Figs. 7, 8.

This species was placed in the synonymy of *Vernonia arborescens* (L.) Swartz by Keeley (1982), but her concept is overly broad. Typical West Indian *Lepidaploa arborescens* and continental *L. canescens* are somewhat similar in aspect, but they are not considered to be close relatives in this study. The continental species has characteristically larger leaves and has smaller, more pubescent involucres. The West Indian *L. arborescens* characteristically has foliose bracts at the immediate bases of the heads, but the continental *L. canescens* essentially lacks such bracts. In the few cases where foliose bracts occur in *L. canescens* (Panama, King 5256, US), they are attached on the opposite side of the stem from the heads. The achene surfaces in *L. canescens* have resiniferous idioblasts, whereas those of *L. arborescens* have glands instead. The synonymy of Keeley is redistributed between the two species.

Lepidaploa canescens var. **opposita** (H. Robinson) H. Robinson, comb. nov.

Vernonia canescens var. *opposita* H. Robinson, Phytologia 49:261. 1981. Colombia.

Lepidaploa carachensis (Badillo) H. Robinson, comb. nov.

Vernonia carachensis Badillo, Ernstia 48: 41. 1988. Venezuela. Pollen C/G.

Lepidaploa chalybaea (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia chalybaea Mart. ex DC., Prodr. 5: 54. 1836. Brazil (Bahia, Ceará). Pollen D, Figs. 43–47.

Lepidaploa chamissonis (Less.) H. Robinson, comb. nov.

Vernonia chamissonis Less., Linnaea 4:304. 1829. *V. parodii* Cabrera, Darwiniana 5: 187. 1941. Brazil (Paraná, Santa Catarina, São Paulo), Argentina (Chaco), Paraguay. Pollen C.

Lepidaploa chrysotricha (Alexander) H. Robinson, comb. nov.

Vernonia chrysotricha Alexander, Lloydia 2:217. 1939. Guyana. Pollen C/G.

Lepidaploa cleocalderonae (H. Robinson) H. Robinson, comb. nov.

Vernonia cleocalderonae H. Robinson, Phytologia 46:108. 1980. Brazil (Amazonas). Pollen C, Figs. 17, 18.

Lepidaploa commutata (Ekman) H. Robinson, comb. nov.

Vernonia commutata Ekman, Ark. Bot. 13(15):77. 1914. Cuba. Pollen C.

Lepidaploa complicata (Wright ex Griseb.) H. Robinson, comb. nov.

Vernonia complicata Wright ex Griseb., Cat. Pl. Cub. 143. 1866. Cuba. Pollen C.

Lepidaploa cordiaefolia (H.B.K.) H. Robinson, comb. nov.

Vernonia cordiaefolia H.B.K., Nov. Gen. Sp., folio ed. 4:29. 1818. Colombia. Pollen C.

Lepidaploa costanensis (Badillo) H. Robinson, comb. nov.

Vernonia costanensis Badillo, Ernstia 23:32. 1984. Venezuela. Pollen C.

Lepidaploa costata (Rusby) H. Robinson, comb. nov.

Vernonia costata Rusby, Mem. Torrey Bot. Club 6:53. 1896. Peru, Bolivia. Pollen G.

Lepidaploa cotoneaster (Willd. ex Spreng.) H. Robinson, comb. nov.

Conyza cotoneaster Willd. ex Spreng., Syst. Veg. 3:509. 1826. *Vernonia cotoneaster* (Willd. ex Spreng.) Less., Linnaea 4:298. 1829. *V. axilliflora* Less., Linnaea 4:297. 1829. *V. debilis* Mart. ex DC., Prodr. 5: 54. 1836. Brazil (Bahia, Minas Gerais). Pollen C, Figs. 9–12.

Lepidaploa coulonioides (H. Robinson) H. Robinson, comb. nov.

Vernonia coulonioides H. Robinson, Phytologia 49:263. 1981. Brazil (Rio de Janeiro). Pollen G.

Lepidaploa crassifolia (Rusby) H. Robinson, comb. nov.

Vernonia crassifolia Rusby, Bull New York Bot. Gard. 8:124. 1912. Bolivia. Pollen G.

Lepidaploa cuiabensis (Baker in Mart.) H. Robinson, comb. nov.

Vernonia cuiabensis Baker in Mart., Fl. Bras. 6(2):37. 1873. Brazil (Mato Grosso). Pollen D.

Lepidaploa danielis (Cuatr.) H. Robinson, comb. nov.

Vernonia danielis Cuatr., Bot. Jahrb. Syst. 77:54. 1956. Colombia. Pollen C.

Lepidaploa decumbens (Gardner) H. Robinson, comb. nov.

Vernonia decumbens Gardner, London J. Bot. 4:115. 1845. Brazil (Espirito Santo, Rio de Janeiro, São Paulo). Pollen G.

The species is close to *Lepidaploa subsquarrosa,* which has been known as *Vernonia geminata* Less., but the stems are stouter and straighter, the leaves are more pointed, and the inflorescence is denser.

Lepidaploa deflexa (Rusby) H. Robinson, comb. nov.

Vernonia deflexa Rusby, Bull. New York Bot. Gard. 4:376. 1907. Bolivia. Pollen G.

Lepidaploa densipaniculata (Rusby) H. Robinson, comb. nov.

Vernonia densipaniculata Rusby, Bull. New York Bot. Gard. 8:126. 1912. Bolivia. Pollen G.

Only the type (Cargadira, Williams 1534, NY) and one recent collection (La Paz, Murillo, below Lago Zongo dam, Solomon 10740, MO, US) have been seen.

Lepidaploa desiliens (Gleason) H. Robinson, comb. nov.

Vernonia desiliens Gleason, Bull. Torrey Bot. Club 40:316. 1913. Cuba. Pollen C.

Lepidaploa edmundoi (Barroso) H. Robinson, comb. nov.

Vernonia edmundoi Barroso, Arq. Jard. Bot. Rio de Janeiro 17:21. 1959. Brazil (Bahia). Pollen D.

Lepidaploa ehretiifolia (Benth.) H. Robinson, comb. nov.

Vernonia ehretiifolia Benth., London J. Bot. 2:39. 1840. *V. schomburgkiana* Sch.Bip., Linnaea 20:509. 1847. Guyana, Venezuela. Pollen C/G.

Lepidaploa ekmanii (Urban) H. Robinson, comb. nov.

Vernonia ekmanii Urban, Ark. Bot. 17(7): 62. 1921. Haiti. Pollen C/G.

Lepidaploa eriolepis (Gardner) H. Robinson, comb. nov.

Vernonia eriolepis Gardner, London J. Bot. 5:224. 1846. *V. riedelii* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):64. 1873. Brazil (Ceará, Mato Grosso, Minas Gerais, Paraná, Santa Catarina, São Paulo). Pollen G.

Lepidaploa ferreyrae (H. Robinson) H. Robinson, comb. nov.

Vernonia ferreyrae H. Robinson, Phytologia 45:158. Feb. 1980. *V. apurimacensis* S. B. Jones, Fieldiana, Bot. N.S. 5:38. Dec 1980. Peru. Pollen C.

Lepidaploa fieldiana (Gleason) H. Robinson, comb. nov.

Vernonia fieldiana Gleason, Bull. Torrey Bot. Club 59:374. 1932. Peru. Pollen G.

Lepidaploa fournetii (H. Robinson & B. Kahn) H. Robinson, comb. nov.

Vernonia fournetii H. Robinson & B. Kahn, Phytologia 58:252. 1985. Bolivia. Pollen G.

Lepidaploa frangulaefolia (H.B.K.) H. Robinson, comb. nov.

Vernonia frangulaefolia H.B.K., Nov. Gen. Sp., folio ed. 4:29. 1818. Colombia. Pollen C.

Lepidaploa fruticosa (L.) H. Robinson, comb. nov.

Conyza fruticosa L., Sp. Pl. ed. 2. 1209. 1763. *Vernonia fruticosa* (L.) Swartz, Fl. Ind. Occid. 3:1323. 1806. *V. buchii* Urban, Repert. Spec. Nov. Regni Veg. 16: 146. 1919. Hispaniola. Pollen C; N = 17 (Keeley 1978).

Lepidaploa glabra (Willd.) H. Robinson, comb. nov.

Conyza glabra Willd., Sp. Pl. 3:1940. 1803, non *Vernonia glabra* Vatke, 1877. *Eupatorium obtusifolium* Willd., Sp. Pl. 3: 1768. 1803, non *Vernonia obtusifolia* Less., 1829. *Vernonia albicaulis* Vahl ex Pers., Syn. Pl. 2(2):404. 1807. *V. longifolia* Pers., Syn. Pl. 2(2):404. 1807. *Lepidaploa lanceolata* Cass., Dict. Sci. Nat. 26:17. 1823, nom. inval., prior to validation of *Lepidaploa* at generic level. *Vernonia punctata* Swartz ex Wikstr., Kongl. Vetensk. Acad. Handl. 1827:72. 1828. *V. emarginata* Wikstr., Kongl. Vetensk. Acad. Handl. 1827:73. 1828. *V. vahliana* Less., Linnaea 4:306. 1829. *Eupatorium secundiflorum* Bertero ex DC., Prodr. 5: 48. 1836. *V. thomae* Benth. ex Oerst, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1852:66. 1853. *V. longifolia* var. *sintenisii* Urban, Symb. Antill. 1:456. 1899. *V. sintenisii* (Urban) Gleason, Bull. New York Bot. Gard. 4:187. 1906. *Vernonia gleasonii* Ekman, Ark. Bot. 13(15): 54. 1914. *V. shaferi* Gleason, Bull. Torrey Bot. Club 46:238. 1919. Puerto Rico, Lesser Antilles. Pollen C; N = 17 (Keeley 1978).

In *Lepidaploa,* the oldest name can be used for this species, even though it (and a second older name) are blocked from use in *Vernonia* by being later homonyms. *Vernonia albicaulis* remains the proper name for the species in *Vernonia.*

Lepidaploa gnaphaliifolia (A. Rich.) H. Robinson, comb. nov.

Vernonia gnaphalifolia A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba, Bot. 2:33. 1850. *V. membranacea* Griseb., Cat. Pl. Cub. 144. 1866. *V. crassinervia* Wright ex Gleason, Bull. New York Bot. Gard. 4: 180. 1906. *V. sublanata* Gleason, Bull. New York Bot. Gard. 4:177. 1906. *V. sublanata* var. *angustata* Gleason, Bull. New York Bot. Gard. 4:177. 1906. *V. angustata* (Gleason) Gleason, Bull. Torrey Bot. Club 40:309. 1913. *V. gnaphaliifolia* var. *platyphylla* Gleason, Bull. Torrey Bot. Club. 46:238. 1919. *V. platyphylla* (Gleason) Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:100. 1929. *V. nervosa* Alain, Contr. Ocas. Mus. Colegio "De la Salle." 18:150. 1960. Cuba. Pollen C.

Lepidaploa gnaphalioides (Sch.Bip. ex Mart.) H. Robinson comb. nov.

Vernonia gnaphalioides Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):78. 1873. Brazil (Minas Gerais, Paraná). Pollen G.

Lepidaploa gracilis (H.B.K.) H. Robinson, comb. nov.

Vernonia gracilis H.B.K., Nov. Gen. Sp., folio ed. 4:27. 1818. *V. moritziana* Sch.Bip., Linnaea 20:511. 1847. Colombia, Venezuela. Pollen C.

The concept follows Badillo (1984).

Lepidaploa grisea (Baker) H. Robinson, comb. nov.

Vernonia grisea Baker in Mart., Fl. Bras. 6(2):61. 1873. Brazil (Amazonas, Ceará, Pará, Piauhy). Pollen D.

The species seems close to *Lepidaploa arenaria* Gardner, but the latter is basically a costal species with more succulent leaves. Vegetatively the species seems close to *L. obtusifolia* of southern Brazil, but the latter belongs to the group with type C pollen. The latter further differs by the rather indistinct cymes in the inflorescence with little or no reduction in the size of the bracts of the inflorescence.

Lepidaploa hagei (H. Robinson) H. Robinson, comb. nov.

Vernonia hagei H. Robinson, Phytologia 45: 176. 1980. Brazil (Bahia). Pollen G.

Lepidaploa harrisii (S. Moore) H. Robinson, comb. nov.

Vernonia harrisii S. Moore, J. Bot. 66:164. 1928. Jamaica. Pollen C.

Lepidaploa helophila (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia helophila Mart. ex DC., Prodr. 5: 50. 1836. *V. subcordata* Gardner, London J. Bot. 5:226. 1846. Brazil (Bahia, Mato Grosso, Minas Gerais, São Paulo). Pollen G.

The distribution and synonymy is taken from Baker (1873), but such a range seems unlikely for a species so poorly represented in collections. A specimen from Bahia (Harley 18497, US) may be this species; it has glands on the anthers with one or two glands on the apical appendages. The material shows no other important characters of the comparatively remotely related genus *Chrysolaena* (Robinson 1988b).

Lepidaploa jenssenii (Ekman ex Urban) H. Robinson, comb. nov.

Vernonia jenssenii Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:98. 1929. Cuba. Pollen C.

Lepidaploa karstenii (Sch.Bip.) H. Robinson, comb. nov.

Vernonia karstenii Sch.Bip., Linnaea 30: 169. 1859. Colombia. Pollen C.

Lepidaploa lehmannii (Hieron.) H. Robinson, comb. nov.

Vernonia lehmannii Hieron., Bot. Jahrb. Syst. 19:44. 1894. *Vernonia larensis* Badillo, Bol. Soc. Venez. Ci. Nat. 10:285. 1946. Venezuela, Colombia, Ecuador. Pollen C.

Lepidaploa leptoclada (Sch.Bip.) H. Robinson, comb. nov.

Vernonia leptoclada Sch.Bip., J. Bot. 1:233. 1863. Cuba. Pollen C.

Lepidaploa liesneri (H. Robinson) H. Robinson, comb. nov.

Vernonia liesneri H. Robinson, Phytologia 49:264. 1981. Venezuela. Pollen C.

Material of this species was the basis for Badillo's (1982) report of the Colombia *Vernonia marguana* Cuatr. from Venezuela. The two species are vegetatively nearly alike and must be closely related. The Colombian species differs by having more robust inflorescences with larger heads bearing more than twice as many flowers (over 20 vs. 8–9) and by bearing more numerous, shorter involucral bracts.

Lepidaploa lilacina (Mart. ex DC.) H. Robinson, comb. nov.

Vernonia lilacina Mart. ex DC., Prodr. 5: 48. 1836. *V. adamantium* Gardner, London J. Bot. 5:222. 1846. Brazil (Bahia, Minas Gerais). Pollen C.

Lepidaploa luetzelburgii (Mattf.) H. Robinson, comb. nov.

Vernonia luetzelburgii Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 9:377. 1925. Brazil (Piauhy). Pollen D?

A type photograph shows a species close in habit and pubescence to the more recently described *Lepidaploa pinheiroi* of Bahia, but the leaf tips are rounded and the involucral bracts lack the long apical spines of the latter species.

Lepidaploa macahensis (Glaziou ex Barroso) H. Robinson, comb. nov.

Vernonia macahensis Glaziou ex Barroso, Arq. Jard. Bot. Rio de Janeiro 17:21. 1962. Brazil (Espirito Santo, Rio de Janeiro). Pollen C.

I place here also material in herbaria under the name *Vernonia tijucana* Glaziou from Rio de Janeiro. The latter name was never validated by either Glaziou or by Ekman. The lack of validation is in spite of some annotations by Ekman indicating his intention to publish the name. The Barroso publication was the first and only validation for either Glaziou name. Material under the name *V. tijucana* seems to have more entire leaves and more spreading cymose branches compared to typical *Lepidaploa macahensis*, but the differences do not seem worthy of species rank.

Lepidaploa mandonii (Sch.Bip. ex Gleason) H. Robinson, comb. nov.

Vernonia mandonii Sch.Bip. ex Gleason, Amer. J. Bot. 10:300. 1923. Bolivia. Pollen C.

Lepidaploa mapirensis (Gleason) H. Robinson, comb. nov.

Vernonia mapirensis Gleason, Amer. J. Bot. 10:307. 1923. Bolivia, Peru. Pollen G.

The species is redelimited to exclude *Lepidaploa trichoclada* that was placed in synonymy by Jones (1980) and exclude the numerous specimens of *L. sordidopapposa* recently annotated by Jones as *Vernonia mapirensis*. The present species, as seen in the type (Buchtien 1533, US) and paratype (Buchtien 2462, US), has leaves similar to *L. canescens*, but the heads are somewhat larger and more densely arranged, the pap-

pus is dirty yellowish, the surfaces of the achenes lack resiniferous idioblasts, and the pollen seems consistently to be type G. One specimen from Paucatambo, Dept. Cuzco, Peru (Vargas 15495, US) seems to be the same species. *Lepidaploa mapirensis* seems closest to *L. tristis,* but the latter is larger, has more erect or retrorse pubescence on the stems, oblong elliptical leaves with the lateral veins widely separated, and heads that are often paired at the nodes.

Lepidaploa mucronifolia (DC.) H. Robinson, comb. nov.

Vernonia mucronifolia DC., Prodr. 5:55. 1836. Brazil (Bahia). Pollen D.

The species seems very similar in aspect to *Lepidaploa obtusifolia* of the Rio de Janeiro area, but the two are apparently not closely related. The present species is a member of the group having Type D pollen and is a more pubescent plant with less obviously striated stems.

Lepidaploa muricata (DC.) H. Robinson, comb. nov.

Vernonia muricata DC., Prodr. 5:55. 1836. Brazil (Minas Gerais, Rio de Janeiro, São Paulo). Pollen G.

Lepidaploa myriocephala (DC.) H. Robinson, comb. nov.

Vernonia myriocephala DC., Prodr. 5:40. 1836. Peru. Pollen C.

The species was placed in the synonymy of *Lepidaploa arborescens* with *L. canescens* by Keeley (1982), but the leaves are less pubescent and the secondary veins are less closely and less regularly arranged.

Lepidaploa nitens (Gardner) H. Robinson, comb. nov.

Vernonia nitens Gardner, London J. Bot. 5: 221. 1846. Brazil (Bahia, Goiás). Pollen D.

Lepidaploa obtusifolia (Less.) H. Robinson, comb. nov.

Vernonia obtusifolia Less., Linnaea 4:308. 1829. Brazil (Rio de Janeiro). Pollen C.

The species superficially resembles some members of the genus from farther north, such as *Lepidaploa grisea* and *L. mucronifolia.* The latter, however, have Type D pollen, and they are not closely related.

Lepidaploa orbicularis (Alain) H. Robinson, comb. nov.

Vernonia orbicularis Alain, Contr. Ocas. Mus. Colegio "De la Salle" 18:15. 1960. *V. leonis* Alain, Contr. Ocas. Mus. Colegio "De la Salle" 18:14. 1960. Cuba. Pollen C.

Lepidaploa pallescens (Gleason) H. Robinson, comb. nov.

Vernonia pallescens Gleason, Bull. New York Bot. Gard. 4:192. 1906. Lesser Antilles. Pollen C.

Lepidaploa pari (Badillo) H. Robinson, comb. nov.

Vernonia pari Badillo, Bol. Soc. Venez. Ci. Nat. 10:284. 1946. Venezuela. Pollen C.

Lepidaploa persericea (H. Robinson) H. Robinson, comb. nov.

Vernonia persericea H. Robinson, Phytologia 44:292. 1979. *V. cognata* var. *lundiana* Baker in Mart., Fl. Bras. 6(2):95. 1873. Brazil (Bahia, Espirito Santo, Minas Gerais, Rio de Janeiro). Pollen G, Figs. 32, 33.

Lepidaploa persicifolia (Desf.) H. Robinson, comb. nov.

Vernonia persicifolia Desf., Cat. Pl. Hort. Par. ed. 3, 400. 1829. *V. acutifolia* Hook., Bot. Mag. 58:t. 3062. 1831. Brazil (Rio de Janeiro). Pollen C.

During much of its taxonomic history, the species has been placed in the synonymy of *Vernonia sericea* L. C. Rich. The latter entity seems to be exclusively West Indian and has no particular resemblance to the present large-leaved species with its large, remote heads.

Lepidaploa pineticola (Gleason) H. Robinson, comb. nov.

Vernonia pineticola Gleason, Bull. New York Bot. Gard. 4:176. 1906. Cuba. Pollen C/G.

Lepidaploa pinheiroi (H. Robinson) H. Robinson, comb. nov.

Vernonia pinheiroi H. Robinson, Phytologia 45:179. 1980. Brazil (Bahia). Pollen D.

Lepidaploa pluvialis (Gleason) H. Robinson, comb. nov.

Vernonia pluvialis Gleason, Bull. Torrey Bot. Club 40:312. 1913. *V. reducta* Gleason, Bull. Torrey Bot. Club 40:313. 1913. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa proctorii (Urbatsch) H. Robinson, comb. nov.

Vernonia proctorii Urbatsch, Syst. Bot. 14: 589. 1989. Puerto Rico. Pollen C/G.

Lepidaploa psilostachya (DC.) H. Robinson, comb. nov.

Vernonia psilostachya DC., Prodr. 5:43. 1836. *V. oxylepis* Sch.Bip. ex Baker in Mart., 6(2):70. 1973. Brazil (Paraná, São Paulo). Pollen B/G, Figs. 25–27.

Lepidaploa purpurata (Gleason) H. Robinson, comb. nov.

Vernonia purpurata Gleason, Bull. Torrey Bot. Club 40:322. 1913. *V. praestans* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26:101. 1921. Cuba. Pollen C/G.

Lepidaploa reflexa (Gardner) H. Robinson, comb. nov.

Vernonia reflexa Gardner, London J. Bot. 5:228. 1846. Brazil (Bahia, Minas Gerais). Pollen D.

Lepidaploa remotiflora (L. C. Rich) H. Robinson, comb. nov.

Vernonia remotiflora L. C. Rich., Actes Soc. Hist. Nat. Paris 1:112. 1792. *V. sessiliflora* Willd. ex Less., Linnaea 4:309. 1829. *V. tricholepis* DC., Prodr. 5:54. 1836. *V. acilepis* Benth. ex Oerst., Vidensk. Meddel. Naturhist. Foren, Kjøbenhavn 1852: 68. 1853. *Vernonia lithospermoides* Baker in Mart., Fl. Bras. 6(2):66. 1873. *V. hirtiflora* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):70. 1873. *V. setososquamosa* Hieron., Bot. Jahrb. Syst. 22:684. 1897. Venezuela, Guyana, Cayenne, Brazil, Paraguay, Bolivia, Argentina. Pollen G.

A type photograph of *Vernonia ovata* Less. shows a plant from Brazil that is possibly related to *Lepidaploa remotiflora,* but it has broadly elliptical leaves and broader heads with recurved rather than straight outer bracts.

Lepidaploa retrosetosa (H. Robinson) H. Robinson, comb. nov.

Vernonia retrosetosa H. Robinson, Phytologia 45:159. 1980. Peru. Pollen G.

Lepidaploa rigida (Swartz) H. Robinson, comb. nov.

Conyza rigida Swartz, Prodr. 113. 1788. *Vernonia rigida* (Swartz) Swartz, Fl. Ind. Occid. 3:1322. 1806. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa rimachii (H. Robinson) H. Robinson, comb. nov.

Vernonia rimachii H. Robinson, Phytologia 49:266. 1981. Peru. Pollen G.

Lepidaploa rufogrisea (St. Hil.) H. Robinson, comb. nov.

Vernonia rufo-grisea St. Hil., Voy. Distr. Diam. 2:453. 1833. *V. fruticulosa* Mart. ex DC., Prodr. 5:53. 1836. *V. eremophila* Mart. ex DC., Prodr. 5:54. 1836. *V. tricephala* Gardner, London J. Bot. 5:223. 1846. *V. resinosa* Gardner, London J. Bot. 6:419. 1847. *V. saxicola* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):81. 1873. ?*V. oreophila* Malme, Kongl. Svenska Vetenskapsakad Handl. N.S. 32(5):26. 1899. Brazil (Bahia, D.F., Goiás, Mato Grosso, Minas Gerais). Pollen D, Figs. 48–51.

A photograph of the type shows that the older St. Hilaire name applies to the same common species usually known as *Vernonia fruticulosa* Mart. ex DC. The leaves seem to vary in shape from broadly elliptical to linear. A type photograph of *V. oreophila* Malme, of Mato Grosso, seems to represent the same or a closely related species. The leaves of the latter are exclusively ovate and the inflorescences contain very few heads.

Lepidaploa sagraeana (DC.) H. Robinson, comb. nov.

Vernonia sagraeana DC., Prodr. 5:55. 1836. *V. valenzuelana* A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba. Bot. 11:33. 1850. *V. inaequiserrata* Sch.Bip., J. Bot. 1:131. 1863. *V. fallax* Gleason, Bull. Torrey Bot. Club 40:324. 1913. *V. aceratoides* Gleason, Bull. Torrey Bot. Club 40:325. 1913. *V. angusticeps* Ekman, Ark. Bot. 13(15): 14. 1914. *V. linguaefolia* Ekman, Ark. Bot. 13(15):19. 1914. *V. reedii* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26: 97. 1929, not *V. reedii* Daniels, 1907. *V. potrerillona* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26:98. 1929. Cuba. Pollen C/G.

Lepidaploa salzmannii (DC.) H. Robinson, comb. nov.

Vernonia salzmannii DC., Prodr. 5:55. 1836. *V. poeppigiana* DC., Prodr. 5:55. 1836, non *V. poeppigiana* DC., Prodr. 5: 20. 1836. *V. argyropappa* H. Buek., Ind. Gen. Sp. Syn. in DC., Prodr. 2: Praef. v. 1840. *V. miersiana* Gardner, London J. Bot. 4:115. 1845. *V. virens* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):71. 1873. *V. velutina* Hieron., Bot. Jahrb. Syst. 22: 697. 1897. *V. herbertii* Cuatr., Bot. Jahrb. Syst. 77:55. 1956. Central America, Colombia, Peru, Brazil. Pollen C, Figs. 13–16.

Lepidaploa sclareaefolia (Sch.Bip.) H. Robinson, comb. nov.

Vernonia sclareaefolia Sch.Bip., Linnaea 30: 170. 1859. Colombia. Pollen G.

Lepidaploa segregata (Gleason) H. Robinson, comb. nov.

Vernonia segregata Gleason, Bull. Torrey Bot. Club 40:327. 1913. Cuba. Pollen C.

Lepidaploa sericea (L. C. Rich.) H. Robinson, comb. nov.

Vernonia sericea L. C. Rich., Actes Soc. Hist. Nat. Paris 1:112. 1792. *Lepidaploa phyllostachya* Cassini, Dict. Sci. Nat. 26:16. 1823, nom. inval., prior to validation of *Lepidaploa* at generic level. *V. berteriana* DC., Prodr. 5:52. 1836. *Conyza portoricensis* Bertero ex DC., Prodr. 5:52. 1836, nom. nud. *Vernonia racemosa* Delponte, Mem. Reale Acad. Sci. Torino. II, 14: 396. 1854. *V. venusta* Gleason, Bull. New York Bot. Gard. 4:177. 1906. *V. phyllostachya* Gleason, Bull. New York Bot. Gard. 4:181. 1906. *V. angustissima* Wright ex Ekman, Ark. Bot. 13(15):78. 1914. *V. maestralis* Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:99. 1929. Greater Antilles, Virgin Isl. Pollen C, Figs. 4–6; N = 17 (Keeley 1978).

Lepidaploa silvae (H. Robinson) H. Robinson, comb. nov.

Vernonia silvae H. Robinson, Phytologia 46: 112, 1980. Brazil (Pará). Pollen C.

Lepidaploa solomonii H. Robinson, sp. nov.

Plantae suffrutescentes ad 2 m altae. Caule virides striati sparse minute antrorse strigulosi. Folia alterna, petiolis 1.5–2.5 cm longis; laminae ovato-ellipticae 14–16 cm longae et ad 6.5 cm latae base breviter acutae et minime acuminatae margine integrae vel remote minime crenulatae apice breviter anguste acuminatae supra et subtus subglabrae sparse minute strigulosae supra sparsius. Inflorescentiae supra folia vegetativa laxe ramosae seriate cymosae, bracteae foliiformes distincte minores breviter petiolatae petiolis 3–7 mm longis, laminis lanceolatis 3.0–8.5 cm longis et 0.4–2.4 cm latis in ramulis ultimis subnullis. Capitula sessilia solitaria late campanulata ca. 10 cm alta; squamae involucri in partibus atropurpurascentes ca. 45 subimbricatae 4–5-seriatae graduatae exteriores lanceolatae 2–5 mm longae et 0.8–1.0 mm latae apice subaristatae interiores oblong-lineares ad 8 mm longae apice acutae margine omnino minute fimbriatae extus subglabrae vel perminute puberulae. Flores ca. 30 in capitulo. Corollae ca. 7 mm longae extus plerumque glabrae in partibus apicalibus lobarum breviter spiculiferae, tubis cylindricis 3 mm longis, faucibus late infundibularibus 1.0–1.3 mm longis, lobis linearibus ca. 3 mm longis et 0.6–0.7 mm latis; thecae antherarum ca. 2.5 mm longae, appendicibus apicalibus ca. 0.4 mm longae glabrae; basi stylorum abrupte disciformes. Achaenia ca. 3 mm longa dense sericeo-setulifera non glandulifera et non idioblastifera; setae pappi sordide ca. 30 ca. 6 mm longae subdeciduae superne vix latiores in sereibus exterioribus anguste lanceolatae 1.0–1.5 mm longae. Grana pollinis in diametro ca. 45 μm valde lophata, reticulis in typo G. (Fig. 62).

Type.—Bolivia: La Paz: Prov. Murillo, 44.0 km below Lago Zongo dam, vicinity of Cahua hydroelectric plant, 16°03'S, 68°01'W, 1200 m, moist forest, disturbed, alternating with Chacos and secondary forest, shrub, 2 m, 12–15 Sep 1983, J. C. Solomon 10780 (holotype US; isotype MO).

The species resembles *Lepidaploa sordidopapposa* in the dark involucre and the brownish color of the pappus, but it does not seem closely related. The species is distinctive in the subglabrous aspect of the stems and leaves, the narrowly petiolate vegetative leaves, and the lax, seriate cymes with distinct, foliose bracts.

Lepidaploa sordidopapposa (Hieron.) H. Robinson, comb. nov.

Vernonia sordidopapposa Hieron., Bot. Jahrb. Syst. 22:697. 1897. Bolivia, Ecuador, Peru. Pollen G.

The species is extended to include numerous specimens that have recently been annotated as *Vernonia mapirensis* by Jones for his study of the tribe in Peru (Jones 1980). The present species seems to be characterized by the often crowded heads on shortened inflorescence branches, by the involucre remaining nearly cylindrical when dry, and by the dark pappus. The specimens show a great variation in length of the leaf pubescence and density of involucral pubescence.

Lepidaploa sororia (DC.) H. Robinson, comb. nov.

Vernonia sororia DC., Prodr. 5:40. 1836. *V. coulonii* Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):93. 1873. Brazil (Espirito Santo, Rio de Janeiro). Pollen G.

As indicated by Robinson (1987c), the DeCandolle species is not a synonym of *Cyrtocymura scorpioides*, but is an older name for the species that has been known as *Vernonia coulonii*.

Lepidaploa stenophylla (Less.) H. Robinson, comb. nov.

Vernonia stenophylla Less., Linnaea 6:667. 1831. *V. corallophila* Gleason, Bull. Torrey Bot. Club 40:309. 1913. *V. nematophylla* Ekman & Urban, Repert. Spec. Nov. Regni Veg. 26:100. 1929. Cuba, Hispaniola. Pollen C.

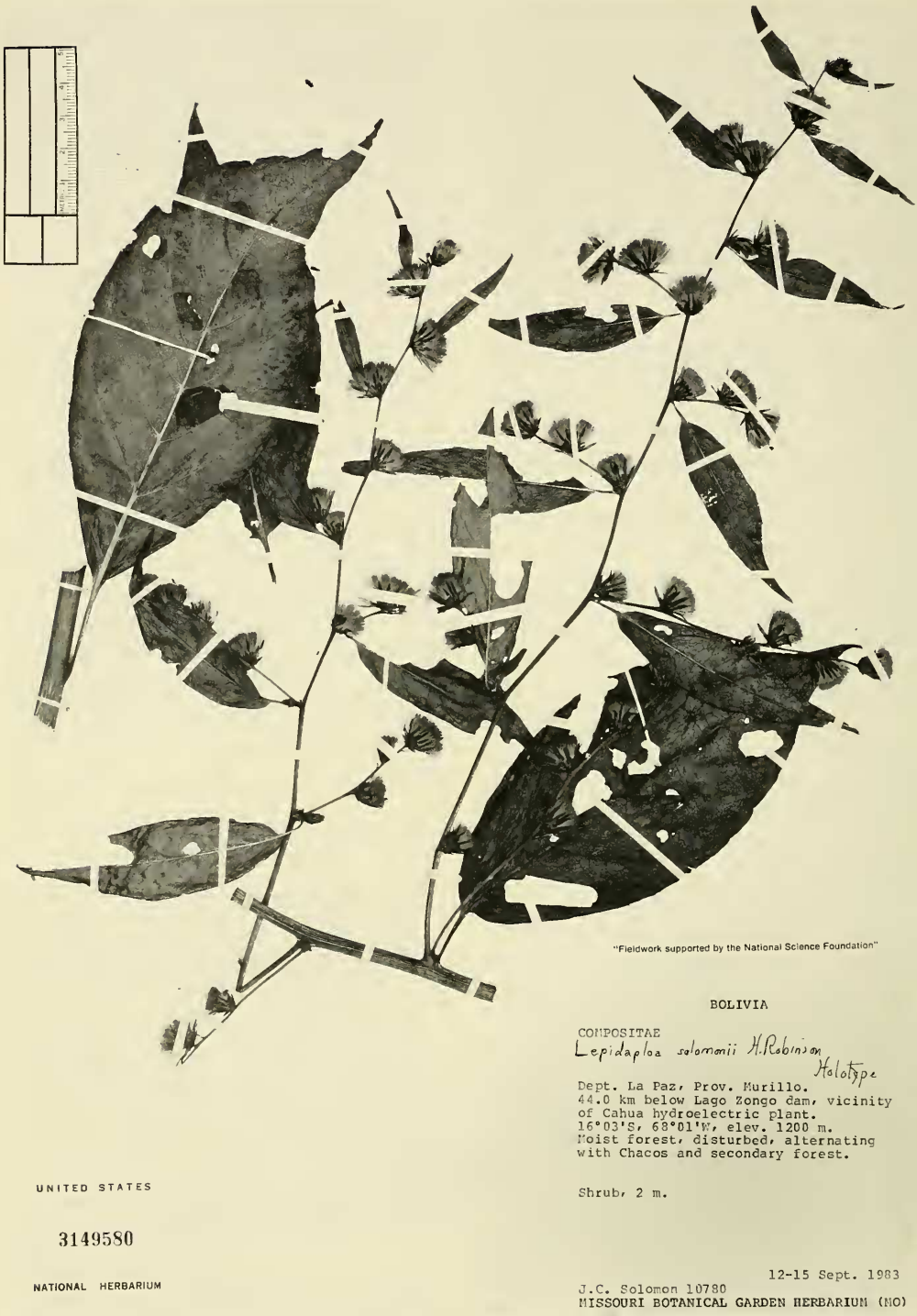


Fig. 62. Holotype of *Lepidaploa solomonii* H. Robinson, Solomon 10780 (US).

Lepidaploa subsquarrosa (DC.) H. Robinson, comb. nov.

Chysocoma paniculata Vell., Fl. Flumin. 327. 1825, non *C. paniculata* [Walter] Gmel. 1792. *Vernonia subsquarrosa* DC., Prodr. 5:41. 1836. *V. albiflora* Gardner, London J. Bot. 6:224. 1847. Brazil (Espirito Santo, Rio de Janeiro, São Paulo). Pollen G, Figs. 28–31.

The species has usually been recognized under the invalid name *Vernonia geminata* Less. Lessing (1829) was not naming a new species but was erroneously identifying Brazilian material as the Colombian *V. geminata* H.B.K. (=*Lepidaploa canescens*). Later attempts (DeCandolle 1836, Baker 1873) to use the name sensu Lessing (exclusively in the atypical sense) were totally invalid. The oldest acceptable name for the species is here raised from synonymy.

Lepidaploa tarijensis (Griseb.) H. Robinson, comb. nov.

Vernonia sericea var. *tarijensis* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24:163. 1879. *V. tarijensis* (Griseb.) Hieron., Bot. Jahrb. Syst. 22:682. 1897. Argentina, Bolivia. Pollen G.

Lepidaploa tenella (D. Nash) H. Robinson, comb. nov.

Vernonia tenella D. Nash, Fieldiana, Bot. 36:74. 1974. Guatemala. Pollen C/G.

Lepidaploa tombadorensis (H. Robinson) H. Robinson, comb. nov.

Vernonia tombadorensis H. Robinson, Phytologia 45:187. 1980. Brazil (Bahia). Pollen D, Figs. 40–42.

Lepidaploa tortuosa (L.) H. Robinson, comb. nov.

Conyza tortuosa L., Sp. Pl. 862. 1753. *C. scandens* Mill., Gard. Dict. ed. 8. *Conyza* no. 11. 1768. *Vernonia schiedeana* Less., Linnaea 6:399. 1831. *V. seemaniana* Steetz, Bot. Voy. Herald 139. 1854. *V. tortuosa* (L.) Blake, Proc. Biol. Soc. Wash. 39:144. 1926. Mexico (Chiapas, Oaxaca, Veracruz), Guatemala, Belize, Honduras, El Salvador, Costa Rica, Panama. Pollen G.

Lepidaploa tovarensis (Gleason) H. Robinson, comb. nov.

Vernonia tovarensis Gleason, Amer. J. Bot. 19:753. 1932. Venezuela. Pollen *Aynia*-type, Figs. 19–24.

Lepidaploa trichoclada (Gleason) H. Robinson, comb. nov.

Vernonia trichoclada Gleason, Bull. Torrey Bot. Club 52:184. 1925. Peru. Pollen G.

This central Peruvian species is resurrected from the synonymy of the Bolivian and southern Peruvian *Lepidaploa mapirensis,* from which it differs in the larger size of the heads, the more erect to retrorse pubescence, and the more oblong leaves with widely separated veins. *Lepidaploa trichoclada* is like the more recently described *L. retrosetosa* of southern Peru in the numerous outer involucral bracts that are as long as the inner bracts. But the latter species has ovate, remotely denticulate leaves with rounded bases and large, foliose bracts in the inflorescence. *Lepidaploa trichoclada* generally resembles the Bolivian *L. tristis,* but the latter has shorter outer involucral bracts and has the heads often paired at the nodes.

Lepidaploa trilectorum (Gleason) H. Robinson, comb. nov.

Vernonia trilectorum Gleason, Bull. Torrey Bot. Club 52:186. 1925. Colombia. Pollen G.

Lepidaploa trinitatis (Ekman) H. Robinson, comb. nov.

Vernonia trinitatis Ekman, Ark. Bot. 13(15): 39. 1914. Trinidad, Venezuela. Pollen C; $N = 51_{II}$ (Keeley 1978).

Lepidaploa tristis (Hieron.) H. Robinson, comb. nov.

Vernonia tristis Hieron., Bot. Jahrb. Syst. 22:683. 1897. Bolivia. Pollen G.

Lepidaploa uniflora (Miller) H. Robinson, comb. nov.

Conyza uniflora Miller, Gard. Dict. ed. 8. *Conyza* no. 13. 1768. *Vernonia ctenophora* Gleason, Bull. Torrey Bot. Club 46: 243. 1919. Mexico (Campeche), Guatemala, Belize. Pollen C.

Lepidaploa urbaniana (Ekman ex Urban) H. Robinson, comb. nov.

Vernonia urbaniana Ekman ex Urban, Repert. Spec. Nov. Regni Veg. 26:99. 1929. Cuba. Pollen C.

Lepidaploa verticillata (Proctor ex Adams) H. Robinson, comb. nov.

Vernonia verticillata Proctor ex Adams, Phytologia 21:409. 1971. Jamaica. Pollen C; N = 17 (Keeley 1978).

Lepidaploa viminalis (Gleason) H. Robinson, comb. nov.

Vernonia viminalis Gleason, Bull. New York Bot. Gard. 4:184. 1906. Cuba. Pollen C/G.

Lepidaploa violiceps (H. Robinson) H. Robinson, comb. nov.

Vernonia violiceps H. Robinson, Phytologia 45:160. 1980. Ecuador. Pollen C.

Lepidaploa virentiformis (Malme) H. Robinson, comb. nov.

Vernonia virentiformis Malme, Ark. Bot. 24A(8):8. 1932. Bolivia (Beni), Brazil (Mato Grosso). Pollen C.

Lepidaploa wrightii (Sch.Bip.) H. Robinson, comb. nov.

Vernonia wrightii Sch.Bip., J. Bot. 1:234. 1863. Cuba. Pollen C/G.

Lepidaploa yunquensis (Gleason) H. Robinson, comb. nov.

Vernonia yunquensis Gleason, Bull. New York Bot. Gard. 4:191. 1906. Cuba.

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Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.